Factors affecting the distribution, abundance and chick survival of the Lapwing (*Vanellus vanellus*)

Thesis

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Factors affecting the distribution, abundance and chick survival of the Lapwing (*Vanellus vanellus*).

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ABSTRACT

This thesis was conducted to investigate Lapwing *Vanellus vanellus* breeding ecology and its relationship with the modern agricultural landscape. Scientific research has suggested that changes in modern agricultural practices have been responsible for the declines in a suite of farmland bird species, including the Lapwing. Fieldwork was conducted over the breeding seasons of 1999 and 2000 over a range of farm locations in Shropshire and Staffordshire, with additional supplementary data obtained from a parallel study undertaken in Cambridgeshire. This research assessed the effectiveness of the 'Lapwing Option' (Option 1B) in the pilot Arable Stewardship agri-environment scheme. A total of 225 nests were located and monitored. There were few detectable effects of agricultural variables on clutch size, egg volume, intra-clutch egg size variation or hatching rates. Cultivation dates stipulated by Option 1B avoided the peak nesting period for this population of Lapwings. At the start of the breeding season Lapwings selected a wide variety of crop types as nest sites, however, crop choice declined as the season progressed, with the majority of replacement nests on Option 1B and spring crops. Lapwings were shown to select nest-sites that had a short, patchy sward structure. Nest survival was high, yet the most common causes of nest failure were predation and losses to agricultural operations. Losses on stubbles and spring cereals were primarily associated with agricultural operations. Nests that were greater than 50m distant from a field boundary had a greater probability of survival than nests that were less than 50m away. Chick weight and condition were shown to be positively correlated with mean egg volume. There was no evidence that any of the measured agricultural variables had an effect on chick growth, condition or survival. Results show that chick survival was low and productivity estimates were less than that required to maintain population stability. Chicks that were known to have fledged had a better body condition index than chicks that had been predated. It was found that the variety of crop types used as foraging habitat declined as the season progressed. Option 1B, set-aside and sugar beet were the latest crops that could be utilised by chicks. A variety of invertebrate taxa were found in faecal samples of chicks, with earthworms, beetles and spiders the most frequent. There was a positive relationship between the number of earthworms in the diet and chick age, chick condition and daily growth rates. Option 1B appears to have a number of benefits for breeding Lapwing, although it does not address low chick survival. Further research is required to elucidate the key factors affecting chick survival and to develop management prescriptions to enhance breeding productivity.

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> "I thank you all most sincerely for all your assistance; and whether or no my thesis may be wretched you have done your best to make it less wretched."
>
> Charles Darwin

AUTHOR'S DECLARATION

This thesis is the work of, and has been written by, the author. No part of this work has been submitted for any other degree or professional qualification.

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CHAPTER 1

INTRODUCTION

1.1 REVIEW OF RELEVANT LITERATURE

1.1.1 Introduction

Lapwings *Vanellus vanellus* are largely terrestrial wading birds, and as the European landscape has been modified by humans for agricultural purposes, the species has adapted to these changes and is now strongly associated with the farmed landscape.

Unlike many farmland species, Lapwings are early breeders with eggs being laid in mid March to early July. They nest on the ground, in open habitats with short vegetation; notably from an agricultural perspective they are strongly associated with spring-drilled crops and short grassland. One brood is raised per season, although there are occasional exceptions (Parish *et al.*, 1997), but if clutch loss occurs females will lay up to four replacement clutches (Klomp, 1954). Three to four eggs are usually laid, which are olive to brown in colour with blotches or streaks usually concentrated at the broad end. The chicks are precocial, that is they leave the nest shortly after hatching and live independent lives, though usually with some form of parental care, such as brooding and guarding (O'Connor, 1984); and they are cared for by both parents. Fledging takes place after 35-40 days, and soon after fledging are totally independent of their parents.

In common with many farmland bird species, Lapwings have declined within, or disappeared from, many lowland areas and this trend has stimulated considerable research into the species' ecological requirements. This research work has recently been reviewed by Hudson *et al.* (1994). This introductory chapter attempts to develop and build on this existing review and complement it with a review of work and papers that have been published since 1994. The focus will be primarily on Lapwing research in an agricultural context, with specific detail on literature pertaining to arable production systems.

1.1.2 Lapwing population trends

1.1.2.1 *Overview*

The Lapwing is a formerly widespread and familiar bird throughout the U.K., and consequently there are some accurate population estimates dating back to the 1960s. Population trends for the species can be identified back to the turn of the 19th century. Gibbons *et al.* (1996) built on extensive reviews by Alexander & Lack (1944) and Parslow (1973) to identify population trends for all breeding bird species, including the Lapwing, in the U.K. since 1800. Throughout the 19th century Lapwings were identified as undergoing a general widespread decrease. From 1900-39 a steady increase was recorded, and from 1940-1995 a gradual decline was identified (Gibbons *et al.*, 1996). Gibbons *et al.* (1996) make no attempt to quantify actual breeding numbers, but solely to identify historical population trends, and ascertain those species of greatest conservation concern. Alexander & Lack (1944) do identify a period of population recovery during the early part of the 20th century coinciding with the implementation of the 1926 Lapwing Act, which restricted the collection of Lapwing eggs, and a period of agricultural recession. Overall it appears Lapwing numbers have been generally decreasing since the 1800s.

1.1.2.2 *1900-1960*

The first large-scale Lapwing survey conducted in Britain in 1937-38 was directed towards identifying habitat selection (Nicholson, 1938, 1939) and no attempt was made to review numbers or identify changes in status. Fisher (1941) was apparently the first to offer a quantitative assessment of the number of breeding pairs, estimated at 175,000 pairs in England and Wales. No revised figure was given in Lapwing monographs by Ennion (1949) or Spencer (1953), though the latter noted a widespread decline in England and Wales during the agricultural revival following the Second World War. This decline was linked to abrupt farming changes, although severe winters of the 1940s, particularly that of 1946/47 (Spencer, 1953) were also implicated.

The 1940s and 50s marked the first phase of the modern agricultural revolution involving mechanisation, land drainage, a major introduction of chemicals, and large areas converted to arable, especially cereal production. The rather meagre information available for this period suggests that after initial adjustment, the national Lapwing population was more or less stable until the early 1960s (Hudson *et al.*, 1994).

1.1.2.3 *1960s -mid 1980s*

The second major study of Lapwing by the British Trust for Ornithology (BTO) was in 1960-61, and summarised in Lister (1964). Local gains and losses in numbers were reported, but it was concluded that there were no marked changes in status. Although Lister identified long-term changes of agricultural policy as being of importance in influencing Lapwing numbers, he found no firm evidence to suggest that agricultural changes were linked to Lapwing population fluctuations. Nevertheless, recent re-analysis of the 1960-61 data (Shrubb & Lack, 1991) suggests that there may have been some regional changes in populations during this period. There were more reports of declines than of increases in northern and south-western counties but more of stability or increases in the arable counties of central, eastern and south-eastern England. However, all regional samples were small (Hudson *et al.*, 1994).

The introduction of the BTO Common Birds Census (CBC) in 1961 has enabled calculation of indices of breeding bird populations. This allows for year-on-year changes in population to be quantified and for population estimates and trends to be determined. Results from CBC data indicated a divergence between Lapwing population trends of northern and southern counties (Sharrock, 1976), with indices suggesting a progressive decline in the south with compensatory increases in the north. However, CBC indices were revised and recalculated after a plot re-selection exercise and a change of datum year (Marchant *et al.*, 1990). The population in southern counties remained relatively stable from 1963 until a marked decline in the mid 1980s, whilst in the northern

counties there was a more consistent pattern of increase that was reversed after 1981. However, any apparent regional differences in CBC data must be treated with caution (Fuller *et al.*, 1985).

During the BTO Breeding Bird Atlas survey period of 1968-72 (Sharrock, 1976) Lapwings were still found to be widely distributed with 91.8% of 10km x 10km squares in Britain and 65.5 % of squares in Ireland occupied by Lapwing pairs. Sharrock (1976) offered an estimate of >200,000 pairs for Britain and Ireland combined. Since this was based on an assumption of 70 pairs/10km x 10km square, and 78.8% of all occupied squares were in Britain, one may attribute 160,000 pairs to Britain alone (Hudson *et al.*, 1994).

During the 1970s and early 80s, the national CBC index for Lapwing fluctuated between relatively narrow limits (Marchant *et al.,* 1990), but after 1984 the index fell sharply and by 1988 it was only half that for ten years earlier (Figure 1.1). Furthermore, populations associated with lowland wet grassland have declined by 38% between 1982 and 1989 (O'Brien & Smith, 1992), probably as a consequence of changes in livestock management.

Marchant *et al.* (1990) considers that changes in agricultural practice to be the driving force behind population declines. This is a plausible explanation when considering surveys associated with non-agricultural habitats, such as the BTO Waterways Bird Survey (WBS), where populations show little overall change between 1979 and 1988 (Marchant *et al.*, 1990).

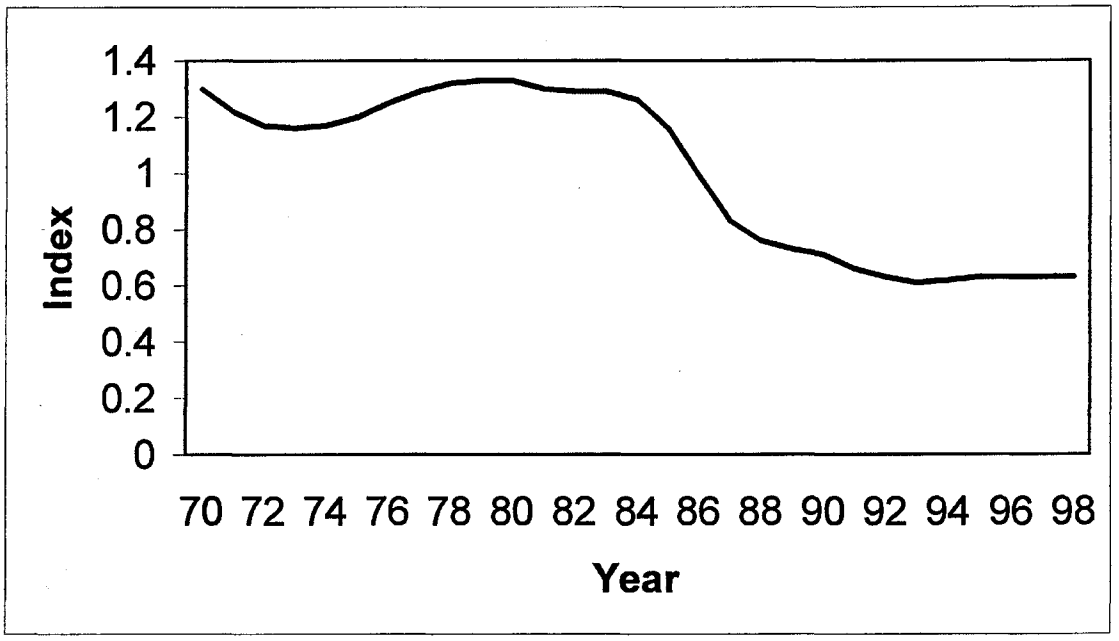

Figure 1.1. Smoothed population indices for Lapwing derived from annual CBC data (data from Baillie *et al.*, (2001), http//www.bto.org/birdtrends).

1.1.2.4 *Mid 80s to present day.*

The numbers and distribution of breeding Lapwings in England and Wales were again surveyed in 1987 by the BTO (Shrubb & Lack, 1991). It was estimated that the Lapwing breeding population of England and Wales for 1987 was 123,000 pairs (95% confidence limits of 110,000 and 136,000), with 96% of pairs on farmland. A clear regional difference was apparent from this study, with regions north of a line from the Humber to Cheshire accounting for 60% of total pairs but comprising about 24% of the total area. For 27 sites that had been surveyed in 1956-65, Shrubb & Lack (1991) compared Lapwing numbers from the 1987 survey. Although there are problems with small sample sizes and a bias towards tillage (Shrubb & Lack, 1991), the downward trend across all regions is consistent (Table 1.1).

Table 1.1. Comparative counts in 1956-65 and 1987 of nesting pairs of Lapwings in 27 areas in England and Wales (after Shrubb & Lack, 1991).

		Pairs counted		
Region	No. of sites	1956-65	1987	Change %
North	2	60	28	-53
Yorks/Humber	5	144	27	-81
North-West	4	78	60	-23
East Midlands	2	87	15	-83
East Anglia	2	6	0	-100
West Midlands	3	34	19	-44
South-East	6	186	82	-56
South-West	2	34	13	-62
Wales	1	8	5	-37
Total	27	637	249	-61

The 1987 survey did not incorporate Scotland, but Galbraith *et al.* (1984) estimated approximately 64,000 pairs of breeding Lapwing on Scottish agricultural land, and Thom (1986) estimated the total population to be between 75,000 and 100,000 breeding pairs. Population change in Scotland is believed to be less marked due to less drastic changes in agriculture practice, but local decreases have been recorded (Thom, 1986; Marchant *et al.*, 1990). The 1988-91 Breeding Bird Atlas (Gibbons *et al.*, 1993) shows the continuing wide distribution of Lapwings, but substantial numbers of 10km x 10km squares in Ireland, western Scotland, south-west Wales and south-west England were unoccupied. A combined British and Irish population was estimated at 205,000 to 260,000 pairs.

1.1.2.5 *1998 BTO/RSPB survey.*

The most recent population survey of the species in 1998, followed the same methodology as the 1987 survey (Shrubb & Lack, 1991) allowing a direct comparison of population changes in the intervening period (Wilson *et al.*, 2001). The overall population estimate for England and Wales was estimated to be approximately 63,000 (62,923 with 95% confidence limits 55,268-74,499), which represents an overall decline of 49% since the 1987 survey (Wilson *et al.*, 2001). Declines were common to all regions but were generally less in northern regions (Yorkshire/Humberside 28% decline) and highest in south-west England (64%); Wales showed the steepest decline of 77% (Wilson *et al.*, 2001). A reduction in range was also evident, with 29% of tetrads holding breeding Lapwings compared with 39% in 1987. The pattern of range reduction is similar to that of the population estimates with only 8% and 11% of tetrads in south-west England and Wales occupied (compared to 21% and 20% respectively in 1987). In northern regions, such as the north-west, 61% of tetrads were occupied compared to 75% in 1987. Overall 39% of all pairs recorded were located on arable farmland and 56% on agricultural grassland highlighting the species' vulnerability to changes in farming practice and landscapes.

1.1.2.6 *Recent trends in Continental Europe*

Lapwings are widespread throughout the whole of Europe (and into north central Asia and north China); and are known to have breeding populations in 34 European countries (Heath *et al.* 2000). Breeding population estimates on a country by country basis are summarised in Heath *et al.* (2000) and vary from as few as 2 pairs in Liechtenstein to as many as 10 million in Russia; a total European breeding population estimate is given as approximately two to eleven million pairs. Population trends within Europe are summarised in Table 1.2.

Table 1.2. Changes in Lapwing breeding population and breeding range by trend categories, across 34 European countries. Data is adapted from Heath *et al.* (2000).

	Number of countries showing	
Trend (1970-90)	Population change	Range change
Large increase (=> 50%)	2[1]	1
Small increase (20-49%)	3[1]	6
Stable (change <20%)	8	14
Small decrease (20-49%)	14	10
Large decrease (=> 50%)	4	1
Fluctuating (no clear trend)	1	1
No trend data	1	1

[1]Population increases have been recorded in Austria, Belarus, Belgium, Italy and Slovenia. With the exception of Belgium, the other countries have not undergone rapid agricultural change as witnessed in other European countries.

1.1.3 Breeding habitat requirements

Cramp & Simmons (1983) identifies a broad variety of habitats used by Lapwings from coastal and estuarine sites, including saltings, mudflats, and sandbanks, to inland areas associated with floodplains, marshes and wet grasslands. However, with the rapid historical encroachment of man on natural habitat types, suitable substitutes have been created largely through agriculture. Although, Lapwings are currently located in a wide variety of habitats, the 1987 and 1998 BTO surveys of breeding Lapwings highlighted the strong association with agricultural land in England and Wales (Shrubb & Lack, 1991; Wilson *et al.*, 2001). In both surveys, spring tillage was strongly favoured and autumn tillage was strongly avoided, with a strong selection for spring tilled fields that were adjacent to grass fields. This finding is consistent with that of other previous BTO studies (Nicholson 1938, 1939, and Lister 1964). Indeed, the trend is of increasing selection for spring tillage with autumn tillage being increasingly avoided. This increased avoidance of autumn tillage is probably linked to intensification of crop management resulting in improved early crop growth and structural homogeneity, rendering the habitat unsuitable for the Lapwing anti-predator defence which relies on good all round vision. The main management changes in autumn sown cereals have been the introduction of tramlining techniques, the use of autumn herbicides, early nitrogen dressings on wheat crops, and the use of foliar fungicides (O'Connor & Shrubb, 1986; Chamberlain *et al.*, 2000). The main impact has been to increase the density and homogeneity of the sward structure in the early stages of the growing season, which coincides with the Lapwing breeding season. There is a strong correlation between the CBC farmland index for Lapwing and the decreasing amount of spring sown cereal (Figure 1.2) (Shrubb, 1990) which further highlights the importance of the switch from spring sowing to autumn sowing.

There is little literature on re-nesting attempts by Lapwings, particularly on arable farmland. Galbraith (1988a) showed the importance of crop growth, even in spring cereals in limiting re-nesting attempts. By early May only fields which have been cultivated unusually late had any nesting birds on them and these birds had apparently suspended breeding and joined post breeding

flocks, but left the flocks and quickly colonised the new bare ground nesting habitat as it became available. This highlights the importance of vegetation growth in curtailing breeding rather than any physiological incapacity of the species. Conversely, nesting attempts on nearby rough grazing continued until late May.

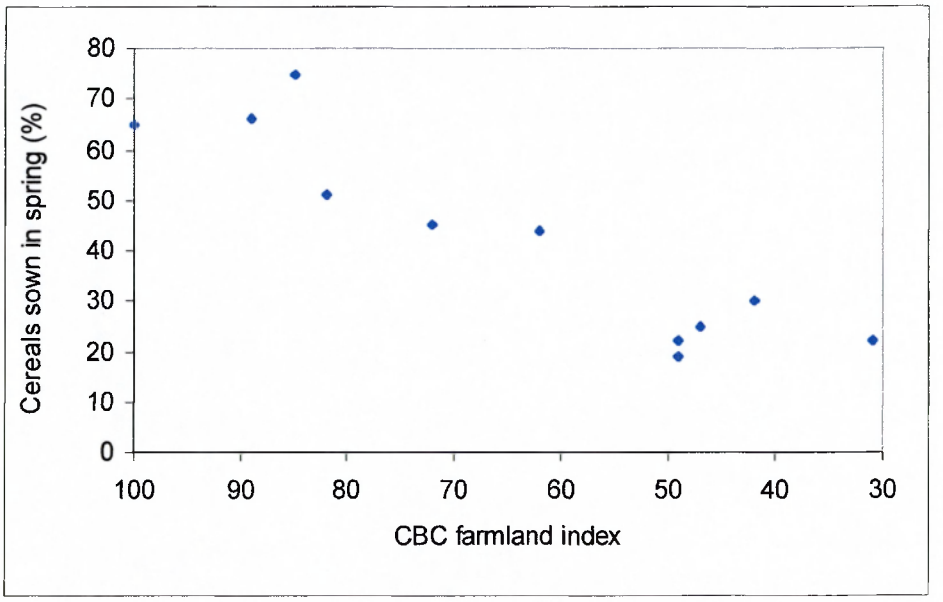

Figure 1.2. The CBC index for Lapwings in the primary cereal growing counties of England and Wales compared to the percentage of spring cereals sown (11 best estimates from the years 1962-1983). The correlation is highly significant: r=0.88, P =<0.01. (Taken from Shrubb 1990).

The improvement of grassland through drainage, re-seeding and the application of inorganic fertilisers has reduced Lapwing densities in pastoral areas. Baines (1988, 1994) found a mean density of 53.9 nesting pairs/100ha on unimproved pasture compared to 14.1 pairs/100ha on improved pasture - a reduction of 74%. Lower Lapwing nesting densities on improved grassland may be ultimately due to the more uniform structure and rapid grass growth that is encouraged (c.f. to autumn sowing on arable). Changes in sward structure are believed to result in increased nest predation (Baines, 1990) and increased stocking densities may lead to reduced breeding success

(Shrubb, 1990) and compound the effect of uniform swards. Wilson *et al.* (2001) showed that Lapwings are associated with rough grazing which has generally been subject to widespread conversion to improved grassland (O'Connor & Shrubb, 1986; Chamberlain *et al.*, 2000). Modern grassland management promotes rapid grass growth, and in some areas this is believed to have been responsible for a shift in the timing of the Lapwing breeding season. In the Netherlands, breeding now begins up to two weeks earlier than was the case at the start of the twentieth century (Bientema *et al.*, 1985). Increased intensification, particularly in terms of encouraging rapid crop growth and density both within arable and grassland systems certainly appear to be reducing the amount of optimal breeding habitat available to Lapwings.

Lapwings exhibit a preference for open landscapes probably as predator avoidance strategy. Milsom *et al.*, (1985) showed that Lapwing habitat use was correlated with the openness of the boundary, although this was not apparent in a study of North Kent grazing marshes (Milsom *et al.* 2000). However, in the same study a negative effect of National Grid power lines was evident and occupancy of the smallest fields by Lapwings was very low, suggesting that Lapwings are able to mediate the presence of vertical structures where fields are of sufficient size. Lapwings show a preference for nest-sites away from trees (potential predator perches and corvid nest-sites) (Berg *et al.*, 1992; O'Brien, 2000) most likely as an evolved response to increased nest survival at greater distances from such features. Suitability of nesting fields are increased if they are near to pasture (Galbraith, 1988a) or damp areas (Berg *et al.*, 1992) which are used as brood rearing areas. Similarly, at the national scale, Wilson *et al.* (2001) show that Lapwings have a strong preference for spring tillage abutting grassland. This 'idyllic' combination represents the key habitat types for the two major components of the Lapwing breeding cycle, i.e. nesting and brood rearing habitat.

1.1.4 Breeding success

1.1.4.1 *Hatching success and general causes of nest failure*

As ground-nesting birds, Lapwings are susceptible to nest loss from a wide variety of sources, particularly losses to predators, and trampling and mechanical operations on agricultural land. The species compensates for these losses by being adapted to lay replacement clutches. Klomp (1951) recorded up to five replacement clutches in an egg removal experiment, and Berg *et al.* (1992) showed the species' ability to replace lost clutches under natural conditions. At the turn of the twentieth century it was likely that there was significant nest loss due to egg collecting, but the implementation of the 1926 Lapwing Act restricted this practice (Alexander & Lack, 1944). The principal causes of nest failure in the modern arable landscape are predation and agricultural operations. Of 1803 eggs laid on farmland in Switzerland 23.5% were predated, 11.5% were deserted, and 6.7% were destroyed by agricultural operations (Glutz von Blotzheim *et al.*, 1975). On marshland in northern Germany (65% arable), 26 % of clutches were predated, 14% lost to agricultural operations and 9% trampled by stock (Matter, 1982).

In Scotland, most egg losses were due to predation or destruction during cultivation. The incidence of these factors varied seasonally and between habitat type. On arable land 59% of nests were predated, and 30% lost to cultivations, whereas on rough grazing there were no losses to cultivation but 89% lost to predators (Galbraith, 1988a). There was a significant difference in hatching success for eggs laid before and after the 15th April (ie during the main cultivation period) on spring cereals, with a 9.3% hatching success prior to the 15th April as opposed to a 53.7% hatching success after the 15th April. Thus the cultivation regime on the arable site apparently resulted in significant reduction in hatching success among birds nesting early. Overall (including rough grazing), Galbraith showed egg predation was the most important cause of failure accounting for 75% of all losses, and hatching success on arable sites was further reduced by egg losses during cultivations.

Berg *et al.* (1992) in central Sweden found that farming operations accounted for 85% of all nest losses, with differences in hatching success varying between habitats: unsown tillage (9% hatching

success), sown tillage (78%), fallow fields (31%) and grassland (67%). Predation accounted for 14% of nest losses. Similarly, Linsley (1999) showed that in an intensively farmed study site in south-west Lancashire, agricultural operations accounted for 77% of nest losses and predation 14%, but it was noted that the study area had intensive predator control in place due to game-rearing interests. Although these results show contrasting results to other studies, such as Galbraith (1988a) and Matter (1982), differences between studies are likely to vary greatly depending on the dominant habitat and land-use, as well as the timing of agricultural operations determined by regional/area specific agronomic practice.

Shrubb (1990) in an analysis of BTO Nest Record Cards showed that variation in nest success between habitats were due to different causes of nest losses. Cereals and bare tilthe were the most successful nesting habitats (71% and 69% nest success respectively) and bare plough and upland improved grass the least successful (43% and 40% respectively). Overall, nests in arable habitats tended to suffer higher nest losses to agricultural operations and nests in grassland habitats suffered more from predation (Table 1.3) (Shrubb, 1990).

In summary, most studies show that Lapwing nest failure rates are relatively high, but the causes vary, although in an agricultural context, farming operations are always important and predation can be significant.

1.1.4.2 *Specific factors influencing nest failure rates*

Specific factors have been alluded to in section 1.1.3, namely, nests that are further away from predator perches (Berg *et al.*, 1992) and corvid nests (O'Brien, 2000) have been shown to have higher daily survival rates. The semi-colonial strategy that many Lapwing populations adopt is perceived to be a further anti-predator adaptation. Berg *et al.* (1992) suggest a general anti-predator effect in large colonies, since nests in colonies were less likely to be robbed than solitary nests and nests in small colonies (less than 5 nests). Furthermore, Goransson *et al.* (1975), Baines (1990), Elliot (1995) and Berg (1996) all recorded lower losses of artificial nests placed within Lapwing colonies compared to those placed outside. However, Berg (1996) questions the validity of using

artificial nests for measuring actual predation rates of real nests. Conversely, Galbraith (1988a) found no relationship between colony size and nest survival (using observations of real nests), which may add weight to Berg's concerns.

It has been suggested that aggressive territory defenders such as Lapwings offer 'protection' to other species nesting within those territories (Dyrcz *et al.*, 1981; Erriksson & Gotmark, 1982). Similarly, Lapwings have been shown to benefit from nesting in multi-species assemblages. Hegyi & Sasvari (1997) found that Lapwing hatching success was highest when nesting in three-species colonies (with Redshank *Tringa totanus* and Black-tailed Godwits *Limosa limosa*).

Predator removal experiments in Wiltshire, suggests that predator control to protect game-birds (Phasianidae) may also benefit other ground nesting birds; Lapwing nest survival increased by 61% (Pearson & Stoate, 1994), although it was not reported if this led to an increase in chick survival and overall productivity. Côté & Sutherland (1995) undertook an extensive review of the scientific literature relating to the impacts of predation on bird breeding success, long-term population viability and the effectiveness of predator control programmes for bird conservation. They concluded from their review of 35 studies of predator removal programmes, that predator removal resulted in enhanced hatching success of the prey species, post-breeding population sizes were only sometimes increased and breeding population sizes remained largely unchanged. From a game management perspective there may be benefits in some instances, but in a conservation context the evidence they reviewed suggested that predator control does not systematically increase breeding bird populations (Côté & Sutherland, 1995).

Table 1.3. The principal causes of nest loss by Lapwings nesting in different farmland habitats in England and Wales from 1962 to 1985, (taken from Shrubb, 1990).

		Number (and %) of nests lost to:			
Habitat	Nests	Desertion	Depredation	Farmwork	Trampling
Upland rough grass	461	74 (16)	101 (22)	21 (5)	37 (8)
Upland improved grass	633	87 (14)	130 (20)	103 (16)	59 (9)
Lowland rough grass	930	62 (7)	208 (22)	39 (4)	51 (6)
Lowland improved grass	710	53 (8)	105 (15)	79 (11)	60 (8)
All grass	2734	276 (10)	544 (20)	242 (9)	207 (8)
All cereals	480	15 (3)	40 (8)	84 (17)	
(Spring cereals)	322	6 (2)	26 (8)	63 (20)	
Bare plough	270	9 (3)	41 (15)	104 (39)	
Bare tilth	93	4 (4)	7 (7)	18 (19)	
Other spring crops	178	13 (7)	6 (3)	59 (33)	
All tillage	1021	41 (4)	94 (9)	265 (26)	
ALL NESTS	3755	317 (8)	638 (17)	507 (13)	207 (6)

1.1.4.3 *Chick survival*

Hudson *et al.* (1994) suggest that in many Lapwing populations chick survival may chiefly determine productivity. The ability of Lapwings to replace lost clutches may lessen the effects of nest loss to predators or agricultural operations. However, high rates of nest loss in May, could influence overall breeding success because late clutches are less likely to be replaced (Matter, 1982). In addition, Klomp & Speek (1971) have shown that Dutch Lapwing chicks hatched later in the breeding season survive as well as earlier chicks. Similarly, Jackson & Jackson (1975) found that although mortality varied from season to season, there was no evidence to suggest that young hatched earlier in the season survived any better or worse than those that hatched later. In their study, the year of lowest chick mortality coincided with the lowest June rainfall of the study years. Furthermore, Hegyi (1996) shows a positive correlation was found between egg volume, hatching weight and chick survival. As many studies on Lapwings show that replacement clutches have smaller egg volumes one would expect a reduced chick survival. Unfortunately, Hegyi did not quantify survival so greater chick mortality later in the breeding season was not apparent.

In contrast, Galbraith (1988a,b) and Linsley (1999) found that chicks which hatched from late clutches grew and survived less well than earlier hatched chicks, and Galbraith suggested this was related to seasonal depletion in food supply. Galbraith (1988b) also shows that egg size influences chick survival up to ten days after hatching. Beyond that age, egg size had no significant effect on survival. The first few days is a critical period for most wader chicks since their thermo-regulatory capabilities are poorly developed. This physiological trait may be further compounded if chicks have to move large distances between hatching sites and foraging sites. Lapwings and other precocial birds compensate for this by laying large eggs, with large yolks and high lipid content that help to sustain them during the first few days from hatching. Any environmental influences that may negatively effect egg size may have a detrimental effect on chick survival.

Baines (1989) found chick survival rates from hatching to fledging increased with age and differed according to habitat type. Chick survival from hatching to four days old was significantly higher on

unimproved land than on improved, although there was no significant difference in the survival rate of chicks from five to ten days old. In the following year differences in chick survival between unimproved and improved grassland continued up to fledging. Overall, chick survival and the timing of mortality were influenced by a combination of habitat effects and differences between years. Comparing grassland data to arable chick survival, Baines (1989) found that chick survival on arable land showed a pattern closer to that of improved grassland, rather than unimproved grassland. Over the two years considered 0.56 Lapwing chicks per pair fledged on arable land, significantly less than the average of 0.86 per pair on unimproved grassland but significantly higher than the 0.25 chicks fledged per pair on improved grassland.

Galbraith (1988a) showed the mortality patterns of chicks to be similar on rough grazing sites and arable, but the extent of the mortality was more severe on the arable sites. Most deaths occurred during the first ten days after hatching. For arable chicks the mortality rate was greatest during the first five to six days when they were being moved on to pasture. Chick survival for arable chicks was influenced by the proximity to pasture. Again there were differences in survival rates between years, attributed to weather patterns retarding crop growth and reducing the need for chicks to move to shorter vegetated pasture fields. Overall, productivity was greatest on rough grazing sites compared to arable, but was different in some years. Thus habitat-specific mortality factors may influence chick survival to varying degrees depending on underlying weather conditions (see section 1.1.4.4).

As would be expected there is much geographic variation in the relative importance of predatory species. The main predators of chicks are gulls (Laridae), crows (Corvidae) and some mammals; and Cramp & Simmons (1983) mentions adult anti-predator responses against raptors, foxes, mustelids and hedgehogs, as well as domestic dogs, livestock and man. Mink and polecat were considered significant predators in Denmark (Iversen, 1986); Carrion crows and black kite in Switzerland (Heim, 1978); carrion crows, stoats and foxes in Scotland (Galbraith, 1988a); daytime predators, probably corvids, in north England (Baines, 1990); and in Sweden corvids were

considered the main predator, with foxes of less importance probably due to low populations during the study as a result of mange (Berg *et al.*, 1992). Beintema & Muskens (1987) note that a drop in vole numbers (Microtus sp.) led to an increase in predation on ground nesting birds (including Lapwings), suggesting a switch in prey items for ground predators. They did not consider predation a major threat despite about half of nests being predated, indeed they found that hatching success per female was high due to the ability to re-nest. Additionally, Heim (1978) noted that there was much annual variation in the extent of predation.

1.1.4.4 *Weather factors affecting chick survival*

There are two main ways in which prevailing weather conditions may effect chicks and chick survival. Firstly, inclement weather conditions may have a negative effect on chick thermo-regulation and increase the need for parental brooding, leaving too little time for foraging and consequently leading to a retardation in chick growth (Beintema & Visser, 1989a,b). Beintema & Visser (1989a) suggest that Lapwing chicks reach thermo-regulatory independence at 70% of fledging age (ie 24-25 days old). Prolonged adverse weather is likely to lead to reduction in chick condition with subsequent high chick mortality. Poor chick condition may lead to an increased susceptibility to predation risk, although there is no published evidence for this. Secondly, chick survival may be affected by indirect weather effects through the reduction in prey availability. Short bouts of wet weather may stimulate invertebrate activity by bringing, for example, earthworms nearer to the soil surface. Conversely, in dry weather the surface invertebrates taken preferentially by Lapwing chicks (notably beetles and insect larvae) become fewer and harder to find so that foraging efficiency is reduced (Matter, 1982). Additionally, during periods of dry weather earthworms burrow deeper and aestivate as the top layers of soil dry out (Edwards & Bohlen, 1986), making them unavailable to both chicks and adults. Again, poor chick condition due to reduced prey availability may render chicks more susceptible to predation.

There may well be some habitat specific micro-climatic effects exerted on chick survival. Chicks foraging on grassland may be susceptible to chilling during wet conditions, from moisture on vegetation. Although this may not be a problem on some arable fields with little vegetation growth, chicks may be exposed more to effects from wind-chill, but this has been little studied.

1.1.5 Adult and chick diet

Lapwing diet consists predominantly of surface and sub-surface invertebrates, with a wide-range of taxonomic groups taken. A wide variety of prey has been reported in the literature (Cramp & Simmons, 1983); insects including beetles, flies, mayflies, crickets and grasshoppers, and earwigs; other prey includes spiders, earthworms, molluscs, millipedes and woodlice. The relative importance of the various taxonomic groups are summarised in Table 1.4.

Table 1.4. A summary of the status of different taxa in the diet of Lapwings. An empty cell denotes that the taxon is not known to be taken as food; hatched cell denotes that the taxon is present in the diet, but not quantified or described as an important dietary component; blacked cell denotes that taxon is present in the diet, and quantified or described as an important dietary component. This data is taken and adapted from Wilson *et al.* (1999).

Inverts.	Pres.	Coleoptera	Pres.	Diptera	Pres.	Hymenoptera	Pres.	Hemiptera	Pres.	Orthoptera	Pres.	Arachnid	Pres.
Mollusca		Carabidae		Tipulidae		Symphyta		Heteroptera		Acrididae		Araneae	
Isopoda		Curculionidae		Culicidae		Cynipidae		Coccoidea		Tettigoniidae		Opiliones	
Annelida		Tenebrionidae		Stratiomyidae		Ichneumonidae		Delphacidae		Gryllidae		Acarina	
Myriapoda		Staphylinidae		Tabanidae		Formicidae		Cicadellidae		Tetrigidae		Pseudoscorpiones	
Arachnida		Chrysomelidae		Sciaridae		Sphecidae		Cicadidae		Gryllotalpidae		Unspecified	
Collembola		Meloidae		Sepsidae		Vespidae		Aphididae		Unspecified			
Ephemeroptera		Buprestidae		Mycetophoridae		Apoidae		Psyllidae					
Odonata		Scarabeidae		Lonchophoridae		Braconidae		Unspecified					
Plecoptera		Histeridae		Agromyzidae		Chalcidoidae							
Orthoptera		Dytiscidae		Opomyzidae		Larvae							
Dyctioptera		Hydrophilidae		Phoridae									
Dermaptera		Geotrupidae		Anthomyzidae									
Hemiptera		Cantharidae		Therevidae									
Psocoptera		Nitidulidae		Drosophilidae									
Thysanoptera		Elateridae		Limonidae									
Neuroptera		Lagridae		Sphaeroceridae									
Mecoptera		Coccinellidae		Chloropidae									
Lepidoptera		Byrrhidae		Scataophagidae									
-Larvae		Scolytidae		Empididae									
Trichoptera		Gyrinidae		Dolichopodidae									
Diptera		Cerambycidae		Asilidae									
-Larvae		Leoidae		Tachinidae									
Hymenoptera		Anthicidae		Chironomidae									
-Larvae		Mordicidae		Syrphidae									
Coleoptera		Lucanidae		Rhagionidae									
-Larvae		Dermestidae		Calliphoridae									
Vertebrata		Cicindelidae		Muscidae									
		Silphidae		Sarcophagidae									
		Unspecified		Bibionidae									
		Larvae		Acalypterata									
				Brachycera									
				Unspecified									

Earthworms are a major food source for adults, and many studies have shown habitat selection and breeding success to be strongly influenced by earthworm densities, particularly during the pre-laying period. The high-energy requirements prior to breeding, for both males (territory formation, defence and courtship) and females (energy reserves for egg formation and incubation), are reflected in the selection of feeding habitats high in prey availability (Galbraith, 1989a; Baines, 1990). Blomqvist & Johansson (1995) showed that females foraged mostly on arable fields where the intake rate of earthworms was high. Högstedt (1974) also showed the importance of earthworms in the diet during the pre-breeding season, and furthermore, that the length of the pre-laying period highly correlated with the abundance of lumbricids (Figure 1.3). In central Sweden, Lapwings selected territories with a high proportion of foraging habitats (Berg, 1993).

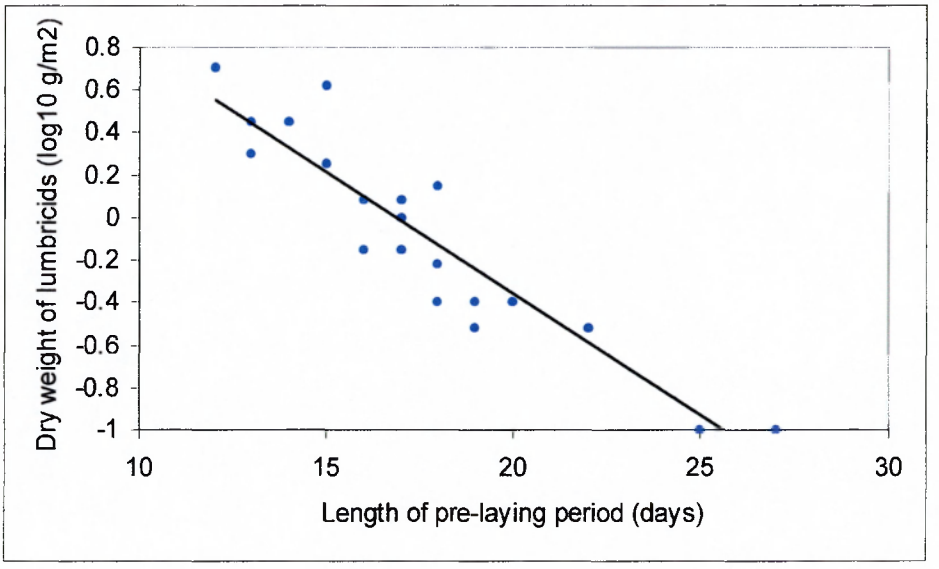

Figure 1.3. Length of the pre-laying period in relation to the availability of earthworms (after Högstedt, 1974). The equation line is represented by $y+0.113x=1.913$, $r=-0.95$, $P=<0.001$

The availability of earthworms is strongly linked to environmental factors, particularly moisture, and as the breeding season progresses and soils dry out earthworms emigrate deeper into the soil (Edwards & Bohlen, 1996). Baines (1990) noted a dietary shift by adult Lapwings with concentration on soil invertebrates (earthworms and insect larvae) in April, switching to surface-active adult invertebrates (especially beetles) thereafter.

The diet of Lapwing chicks is varied and influenced by prey availability and habitat differences in invertebrate communities (Galbraith, 1989b). In Galbraith's study of Scottish agricultural land, rough grazing feeding areas where soil invertebrates (earthworms and leatherjackets) were less abundant, the chicks ate more surface species (mainly beetles and their larvae). And although soil invertebrates composed the major part of the prey biomass, they were taken in comparatively small numbers, which suggests that the chicks were feeding opportunistically rather than selectively. An opportunistic feeding strategy is also noted by Matter (1982) who found a wide spectrum of invertebrate food was taken. Matter (1982) also noted that Lapwing chicks are likely to be found feeding on field perimeters where spiders and larger beetles are most abundant. In which case, there may be a trade-off between foraging near to field boundaries where the risk of predation may well be greater than foraging near central areas of fields where there food may be limiting (cf Berg *et al.*, 1992). Low abundance of earthworms in chick faecal samples in a Swedish study, probably reflected the low earthworm availability at the study site (Johansson & Blomqvist, 1996), but chicks switched to alternative prey items depending on foraging habitat. They also suggest that agricultural intensification may lead to a loss of chick foraging habitats which could be contributing to the decline in not only Lapwing populations, but other waders breeding in agricultural landscapes (Baines, 1988, 1989; Berg, 1992).

Beintema *et al.* (1991) showed that reduced chick growth rates do not correspond with overall prey availability, but there is a requirement to 'switch' to more profitable prey items, such as earthworms, to maintain the required energy intake. Earthworm availability typically declines as the breeding season progresses, as a response to the drying out of soil (Edwards & Bohlen, 1996).

Consequently, for Lapwings there exists an interesting evolutionary trade-off between earlier nesting (potential adverse weather reducing foraging potential) and late nesting (reduced availability of profitable prey items, ie earthworms).

1.1.5.1 *The influence of habitat type and agricultural management on prey abundance and availability.*

1.1.5.1.1 *Earthworms*

The number of earthworms may vary considerably between agricultural habitats (Johansson & Blomqvist, 1996; Galbraith, 1988a; Baines, 1988, 1990), and it is well established that grassland habitats usually contain more earthworms than arable land (Table 1.5). Furthermore, within grassland habitats, the abundance of earthworms is lower on rough grazing than in pasture or other improved grazing (Galbraith, 1988a). Pasture is an important feeding habitat for chicks and access from an arable nesting site can be a critical factor in chick survival (section 1.1.4.3).

It has been shown in many studies that agricultural management has a major effect on earthworm abundance. For example, under conventional tillage the number of earthworms is significantly less than on fields under reduced tillage management (Edwards & Lofty, 1978, 1982a; Barnes & Ellis, 1979; Gerard & Hay, 1979; Brady, 1985; Edwards & Bohlen, 1996; Uri, 1999). It seems that the most important factor controlling earthworm populations in arable land is the amount of organic matter that is available as food for earthworms (Evans & Guild, 1948; Edwards & Bohlen, 1996). Applications of organic farmyard manures increase invertebrate populations in soils quite rapidly (Curry, 1976; Anderson, 1983) and although artificial nitrogenous fertilisers have similar effects, these are more limited (Edwards & Lofty, 1982b; Tucker, 1992; Edwards & Bohlen, 1996).

In general, the decreased use of farmyard manures and increased use of fast acting artificial fertiliser, has led to a decrease in diversity and size of most soil invertebrate populations in arable land (Edwards, 1984). In grassland habitats a large amount of organic matter exists naturally in the soil, and although the application of manures will not necessarily increase the already high

invertebrate densities, they may lead to an increase in earthworm surface activity (Scullion & Ramshaw, 1987) making them more readily available to foraging Lapwings.

Table 1.5. The biomass of earthworms in different habitats (adapted from Edwards & Bohlen, 1996).

Habitat	No./m2	g/m2	Region	Reference
Fallow	22.6	79	Wales	Reynoldson (1966)
Arable	146	50	N. Wales	Reynoldson (1955)
Arable	287	76	Bardsey Island	Reynoldson (1955)
Pasture	389-470	52-110	UK	Svendsen (1957)
Pasture	390	56	Bardsey	Reynoldson et al. (1955)
Pasture	481-524	112-120	N. Wales	Reynoldson (1955)

1.1.5.1.2 *Other invertebrates*

The long running study by the Game Conservancy Trust in Sussex provides some of the best long-term evidence (since 1970) that invertebrate numbers have declined in relation to the intensification of agriculture, particularly the increase in pesticides (Ewald & Aebischer, 1999; Sotherton & Self, 2000). The reduction in the amount of ley grassland and undersowing of cereals is known to have contributed to a reduction in invertebrates, in particular sawflies (Potts, 1986; Aebischer 1990). Changes in management practice, such as cultivation depth and timing, and simplification of crop rotations may have contributed to changes in invertebrate abundance (Sotherton & Self, 2000). Continual intensive cropping and the promotion of homogenous swards typical of modern agriculture has led to a reduction in micro-habitats for a variety of invertebrates. Reduced tillage and direct drilling has been shown to be beneficial for invertebrates by leaving crop residues on the soil surface that may be used as cover and food for a variety of invertebrate species (Brady, 1985; Uri, 1999).

In their review of changes in arthropod abundance on lowland farmland, Sotherton & Self (2000) conclude that more work is needed to link declines to specific agricultural practices so that remedial measures can be trialed and tested to halt and reverse population declines. Even so, probably the

over-riding management change in agricultural landscapes that has had detrimental effects on a whole suite of invertebrates is pesticide usage.

1.1.5.1.3 *Effects of pesticides on food supply*

The greatly increased use of pesticides can be harmful, not only to the target pest species, but also the invertebrate prey populations of the Lapwing. Edwards & Bohlen (1996) reviewed the effects of pesticides and other chemicals on earthworm populations, and also summarised the results of laboratory and field experiments on testing the toxicity of chemicals to earthworms (Edwards & Bohlen, 1996). The carbamate pesticides are toxic to earthworms as are the majority of fumigant and contact nematicides. Although, very few herbicides are directly toxic to earthworms (Edwards, 1989) they may exert considerable indirect effects due to their influence on weeds as a source of organic matter on which earthworms feed in soil.

In their comprehensive review of the indirect effects of pesticides on birds, Campbell *et al.* (1997) show that most individual invertebrate groups have declined in the last 20-30 years. They highlight evidence from a range of studies that the use of pesticides frequently results in considerable short-term reductions in the abundance of target and non target species, and that such effects may persist for weeks or months after the date of application. Furthermore, for a number of declining farmland birds, declines commenced during a period of increasing pesticide use. Although this adds to the evidence for an indirect effect of pesticides on bird populations, it does not imply a causal relationship. However, recent work by Morris (2002) has shown a negative effect of insecticide application on chick food resources, foraging patterns and chick growth in Yellowhammers *Emberiza citrenella*. Furthermore, with a number of studies showing deleterious effects of pesticides on surface dwelling invertebrates (Vickerman & Sunderland, 1977; Sotherton, 1982; Basedow, 1985; Smith & Stratton, 1986; Buchs *et al.*, 1989) the effects upon food availability, particularly in the absence of earthworms late in the season, may have far reaching consequences for adults and chicks alike.

1.1.6 Post-breeding behaviour and post-fledging survival

The Lapwing breeding season generally finishes towards the end of June, although young from late replacement clutches may not fledge until mid July. Birds leave the breeding sites and gather into flocks from mid May onwards consisting initially of failed breeders and non breeders (Cramp & Simmons, 1983) and adults begin their annual moult (Appleton & Minton, 1978; Snow & Snow, 1976). In contrast to continental birds, which may move large distances (Imboden, 1974), British breeders mainly make short summer dispersals (within 100km), though there is some indication of adult movement west/south west into Ireland (Cramp & Simmons, 1983; Wernham *et al.*, 2002). This mobility of post-breeding/post-fledging flocks allows birds to no longer be constrained by limitations in nesting sites, and are able to seek optimum conditions in other habitats and areas. As such, the effect of agricultural practice is not as important as during the breeding season when the birds are tied to nest-sites. However, if limiting food resources on breeding sites may affect the body condition of birds particularly juveniles, this may have an effect on post-fledging survival. Post-fledging survival has been little studied in Lapwings, probably due to their dispersal distance when leaving breeding sites.

1.1.6.1 *Habitat selection*

Milsom *et al.* (1985) showed that Lapwing flocks tend to feed on non-arable sites in June and July when tall crop height limits the use of arable crops but there was an increased use of stubble and plough when harvesting began. Mason & McDonald (1999) found harvested potatoes and pea stubbles to provide key areas for feeding during the summer. A number of studies have found permanent grass to be a preferred feeding habitat in autumn and winter (Fuller & Youngman, 1979; Balança, 1984; Milsom *et al.*, 1985; Tucker, 1992), and is probably linked to the occurrence of high densities of soil invertebrates in permanent grass. Conversely, a preference for winter cereals has been shown in other studies (Gregory, 1987; Shrubb, 1988), particularly in early winter. Mason & McDonald (1999) showed that Lapwings use ploughed fields and stubble in autumn, cereals in

winter and grass to be increasingly important in late winter. Kirby & Fuller (1994) and Village & Westwood (1994) found that pasture was avoided in early autumn, when earthworms were likely to have burrowed deeper into drying soil.

Differences in habitat use between studies during the post-breeding period are likely to be strongly influenced by an area's underlying habitat availability and cropping practice. However, given the high mobility of Lapwings away from breeding sites, Lapwing populations are unlikely to be strongly affected by agricultural land management practices outside the breeding season. Indeed, over-winter survival rates have increased in recent years (section 1.1.7.1).

1.1.7 Lapwing population dynamics

1.1.7.1 *Mortality rates and productivity requirements*

Adult mortality estimates have been calculated from ringing recoveries, for both first year and older adult age classes (Table 1.6). Baines (1989) estimated that to sustain the population about one chick per pair per year should be fledged (based on survival rates of adults of 67% (Haldane, 1952; Lack, 1954)) and first year survival of 63% (Cramp & Simmons, 1983). Galbraith (1988a) suggested that if adult and first year mortalities of Lapwings are similar to those of other waders of similar body size, ie 25-30% and 35-40% respectively, then 0.8 chicks per pair would need to fledge to maintain a stable population. From an analysis of BTO ring recovery data Peach *et al.* (1994) show that Lapwings over-winter survival has increased from 0.663 (period 1930-60) to 0.752 (period 1961-88). The life expectancy for an adult Lapwing has increased from 2.4 years to 3.5 years. This increase in survival represents a 40% increase in the annual breeding potential of the individual. In order to replace annual adult losses, Lapwings need to produce 0.83-0.97 fledged young per pair per year (Peach *et al.*, 1994). All productivity estimates need to be treated with caution as they are likely to vary from year to year depending on broad scale factors such as weather conditions, especially given that first year survival in particular can vary quite dramatically from year to year (Peach *et al.*, 1994). However, the most recent analysis of ring recovery data incorporated weather

co-variates (and declining reporting rates) directly into the modelling procedure (Catchpole *et al.*, 1999). Adult annual survival was shown to be negatively related to measures of winter severity, and the improved survival rate of 0.828 in comparison to 0.752 of Peach *et al.* (1994), is most likely due to milder winters in recent years. The increased adult survival of 13% would suggest that to maintain population stability, the number of young fledged per pair per year needs to be between 0.72 and 0.84. It has been suggested that mortality tends to be overestimated when using ringing recovery data due to ring loss (Soikkeli, 1967; Evans & Pienkowski, 1984), although Peach *et al.* (1994) found no evidence that Lapwing survival rate estimates were affected by ring wear and loss.

Table 1.6. Estimates of Lapwing mortality, derived from studies of ringing recoveries (after Hudson *et al.*, 1994).

Region of sample	1st year mortality (%)	Adult mortality (%)	Reference
Britain & Ireland	37.5	33.9	Glutz von Blotzheim et al., (1975)
Central Europe	40.1	29.4	Glutz von Blotzheim et al., (1975)
Scandinavia	40.4	33.1	Glutz von Blotzheim et al., (1975)
Denmark	c. 44.0	c. 33.0	Bak & Ettrup (1982)
Britain	40.5	24.8	Peach et al. (1994)
Britain	32.8[1]	17.2	Catchpole et al. (1999)

[1]First year survival was not directly determined by Catchpole *et al.* (1999) but factors that led to a 13% increase in adult survival are likely to have had a corresponding effect on first year birds.

Breeding productivity estimates from a number of studies are given in Table 1.7 and show that only 9 out of 23 attain the required levels of productivity to maintain population stability. Measured chick mortality is high and in particular very few of the arable studies (2 out of 7) found sufficient fledging success to maintain populations. Conversely, rough grazing and unimproved grass studies attain the target in most instances (5 out of 7).

Although in Table 1.7 differences in average clutch size are quite small, differences are probably attributable to differing degrees of success in recording partial clutch loss (Hudson *et al.*, 1994) and differences in trampling effects between arable and grassland (Shrubb, 1990).

Wide variations in hatching success between studies (Table 1.7) are attributable to different breeding success in relation to habitat type (eg Galbraith, 1988a; Baines, 1989; Berg *et al.*, 1992). For instance, Baines (1989) found highest hatching success on arable, followed by unimproved grass, and very low hatching success on improved grass; and furthermore these different agricultural land types were all in the same study area, suggesting that habitat specific factors are having significant effects in determining overall breeding productivity.

Table 1.7. Demographic parameters relating to breeding productivity of Lapwings shown by different studies (adapted from Peach *et al.*, 1994). The latest productivity estimates by Catchpole *et al.* (1999) suggest that 0.72-0.84 chicks are required to maintain population stability, studies that achieve this level of productivity are highlighted in bold.

Habitat	Mean clutch size	Hatching success	Fledging success	Productivity	Source
Tillage	3.78	60.0	-	-	Shrubb (1990)
Intensive arable	3.8	39.1	13.9	0.35	Matter (1982)
Arable	3.75	28.2	14.7	0.4	Galbraith (1988a)
Arable	3.74	45.6	23.5	0.57	Baines (1989)
Arable	3.89	55.5	14.7[1]	0.4-0.7	Linsley (1999)
Arable	-	**57.8**	-	**0.7-0.8**	**Beser & Helden-Sarnowski (1982)**
Arable	-	-	-	0.6	Kooiker (1990)
Arable	-	-	-	**1.5**	**van Impe (1988)**
Arable (fallow)	-	-	-	0.5	van Impe (1988)
Mixed farmland	**3.7**	**40.0**	**33**	**0.8**	**Matter (1982)**
Mixed farmland	-	-	-	**2.1**	**Kooiker (1990)**
Mixed farmland	-	-	-	0.6	Imboden (1970)
Mixed farmland	3.79	58.8	14.7	0.33	Onnen (1989)
Mixed farmland	-	63.5	-	0.55	Kooiker (1984)
Mixed farmland	3.6	61.7	13.3	0.23-0.46	French et al. (2000)
Grassland	3.8	53.5	-	-	Liker (1992)
Grass	3.63	51.9	-	-	Shrubb (1990)
Improved meadow	3.61	22.3	21.5	0.23	Baines (1989)
Improved pasture	3.61	16.7	21.5	0.31	Baines (1989)
Rough grazing	**3.75**	**77.9**	**23.9**	**0.88**	**Jackson & Jackson (1980)**
	3.72	65.8	15.0	0.44	Jackson & Jackson (1980)
Marsh	**3.70**	**40.0**	**33.2**	**0.8**	**Matter (1982)**
Rough grazing	**3.74**	**34.3**	**24.4**	**0.8**	**Galbraith (1988a)**
Unimproved pasture	**3.73**	**39.9**	**35.5**	**0.92**	**Baines (1989)**
Unimproved meadow	3.73	32.3	35.5	0.6	Baines (1989)
Grassland	**3.83**	**58.4**	-	**1.6**	**Heim (1978)**

[1]sample incorporating radio-tagged chicks only.

1.1.7.2 *Natal philopatry and sink populations*

Lapwings are known to exhibit a high degree of site faithfulness, returning to sites where they hatched (Spencer, 1953; Heim, 1978; Onnen, 1989; Thompson *et al.*, 1994). Ringing recoveries show about 70% of Lapwings that survive the winter subsequently return within 20km of the natal area (Cramp & Simmons, 1983). Conversely, there are extreme cases when birds ringed in Western Europe (one bird in England, and one bird in Holland) have been recovered the following year in the former USSR, at distances of 4370km and 5170km respectively (in Cramp & Simmons, 1983). This ability for occasional wide dispersal of individuals is believed to prevent sub-speciation between populations across the wide breeding range of the Western Palearctic (Mead *et al.*, 1968). Furthermore, it also enables birds to colonise new localities and maintain breeding numbers in sub-optimal areas where productivity is not sufficient to maintain populations.

The degree of philopatry and site-fidelity amongst most Charadriiformes is poorly understood (Thompson & Thompson, 1991), and indeed only recently has the extent of philopatry and site fidelity been quantified for a Lapwing population (Thompson *et al.*, 1994). Thompson *et al.* (1994) looked at two sites in the north of England, one had a declining population and the other population was stable. Both sites showed high breeding site fidelity amongst adult birds with 95% breeding in the same or an adjacent field in consecutive years. Of these birds, 80% bred in the same field, and the remaining 15% were compelled to breed in adjacent fields, due to crop rotation making natal fields unsuitable. However, second year birds were less site faithful than older adults, with only 58% nesting in the same field in successive years. Furthermore, a smaller proportion of the estimated first years survivors returned to the declining population (37%) compared with a 74% return rate to the stable population and genuine differences in philopatry were presumed. Importantly, late hatching chicks returned less frequently to within 5km of the natal area than earlier hatched chicks or average date chicks, suggesting that late hatching chicks experience higher rates of post-fledging mortality. Thompson *et al.* (1994) suggest that local population density is to a large extent dependent on the number of birds produced locally, and that immigration may in the short-

term bolster a declining population. However, immigration alone would not be sufficient to maintain a population in a stable state in the long-term. The implications from this study suggest that conservation efforts should adopt a metapopulation approach, identifying key source Lapwing breeding populations and encouraging high levels of productivity to help re-colonise deserted or sub-optimal areas.

1.1.7.3 *Metapopulation theory, source-sink concept and density dependence*

Newton (1998) defines the term metapopulation as any population composed of a number of discrete and partly independent sub-populations that live in separate areas that are linked by dispersal. Does this definition apply to Lapwings? The Lapwing in the U.K. is still a widely dispersed species (Wilson *et al.*, 2001) and occurs in the majority of 10km squares as a breeding species (Gibbons *et al.*, 1993). By taking a regional or county level approach, and identifying populations of breeding birds using a colony size threshold (eg 10 pairs per unit area) and then monitoring productivity and year to year population numbers, conservation measures can be implemented to maintain and improve productivity of source populations. A similar approach would be to use an existing nature reserve network as source populations. A recent analysis of population trends of Lapwings on RSPB reserves has shown that breeding numbers have increased by 43% (Ausden, *pers. comm.*), and in some areas reserves are becoming increasingly important refuges. In East Anglia in 1998, RSPB lowland wet grassland reserves supported between 9 and 35% of the regions 1376-5036 pairs of breeding Lapwings (Wilson *et al.*, 2001; Ausden & Hirons, 2002). Density-dependent competition for limited nesting habitat should lead to dispersal into new areas and the formation of new colonies (sub-populations) and recolonisation of sub-optimal habitats previously deserted. However, the concept of metapopulations and source-sink dynamics (Pulliam, 1988) implies that competition between individuals must occur ie there is some form of density-dependent regulation of population levels. Galbraith (1988c) found no evidence for density-dependent effects influencing hatching or fledging success. However, temporal and spatial settlement

patterns of adults in his study conformed to the 'ideal free' (Brown, 1969) and 'ideal despotic' (Fretwell & Lucas, 1970) models, suggesting that territoriality may exert a density-dependent effect through the exclusion of birds seeking territories into sub-optimal habitats where breeding success is low. This may well be more pertinent today when fewer patches of 'ideal' Lapwing breeding habitat are available due to the negative impacts of agricultural changes. Similarly, it may well be difficult to show density-dependent regulation of Lapwing populations as the current low population level may well mask density-dependent effects. Furthermore, density-independent factors, such as weather, may further complicate matters (Galbraith, 1988c). It is worth noting that limitation of breeding densities have been found for a number of Charadriiformes. Parr (1979) found that Golden Plover *Pluvialis apricaria* territories were occupied in sequence and rapidly recolonised if a pair failed or completed breeding and then vacated the territory. Holmes (1970) and Harris (1970) used removal experiments to show rapid recolonisation of removed birds' territories. However, for Lapwings this remains an area requiring further research. It should be noted that density limitation by territorial behaviour and the existence of replacement breeders have been shown in up to 63 of 74 experiments on 53 different bird species (Newton, 1998).

1.2 THE ARABLE STEWARDSHIP PILOT SCHEME

Changes in arable farming over the last few decades have resulted in a loss of wildlife habitats and a general decline in populations of a number of species of birds, insects and plants (Fuller *et al.*, 1995; Wilson *et al.*, 1999; Fuller, 2000; Sotherton & Self, 2000). The aim of the Arable Stewardship Pilot Scheme was to help farmers recreate and enhance wildlife habitats in arable areas. The Pilot Scheme tested whether certain arable farming methods can help achieve this. The scheme was designed to achieve these benefits whilst recognising the practicalities of commercial arable farming. Arable Stewardship was launched in 1998, and was piloted as part of the Countryside Stewardship Scheme (prior to the completion of this thesis a number of options have been incorporated into The Countryside Stewardship Scheme, see Appendix 1). The two pilot areas were in East Anglia and the West Midlands (Figures 1.4 & 1.5). There were five broad management options, and within these there were opportunities for farmers to undertake additional activities and practices that attract additional payments (Table 1.8). Options 1 (over-wintered stubbles) and Option 2 (undersown spring cereals) were the options most likely to have benefits to breeding Lapwings through the provision of nesting habitat (Lapwings are known to have a strong preference for spring tillage, section 1.3.1). Full details of the Pilot Scheme are given in MAFF (1998). Monitoring of the Arable Stewardship Scheme was implemented to ascertain whether a whole suite of options would benefit a wide variety of taxa, including both wintering and breeding birds. The type of survey based monitoring that was adopted was not designed to investigate how the various options may influence demographic parameters and ultimately breeding success.

This PhD. thesis was instigated to target one particular option and it's effect on one particular species. The Lapwing was chosen as the focal species because:

i) it has been identified as being one of number of farmland birds in a current state of decline. Although a relatively well-studied species there are a number of areas

related to its breeding ecology which are relatively poorly understood, particularly in the context of arable farmland.

ii) one of the Arable Stewardship options (1B) has been specifically designed to provide nesting habitat for the species. An assessment of which may lead to an understanding of the mechanisms required to reverse the population decline of this widespread and popular farmland bird.

iii) a review of the literature suggests that the demographic parameters driving the species decline is highly likely to be associated with changes in breeding performance, allowing specific targeting of research effort.

iv) the species lends itself to in depth research and monitoring, with adults, nests and chicks relatively easy to locate visually.

Table 1.8. Prescriptions available under the Arable Stewardship Pilot Scheme. The options highlighted in bold are the main categories, with the supplements that attract higher rates of compensatory payments listed below. The supplements in italics are likely to have some benefit to breeding Lapwings by providing nesting habitat.

Option 1: Over-wintered stubbles
1A Limited herbicide use in cereals or linseed, followed by over-wintered set-aside stubbles
1B Over-wintered cereal or linseed stubbles, followed by spring/summer fallow
1A+B Limited herbicide use in a cereal or linseed crop, followed by over-wintered set-aside stubbles and a spring/summer fallow
1C Over-wintered stubbles followed by a spring crop
1A+C Limited herbicide use in a cereal or linseed crop, followed by over-wintered stubbles and a spring crop
Option 2: Undersown spring cereals
2A Over-wintered stubbles, followed by an undersown spring cereal
2B Undersown spring cereal, followed by a grass ley
2A+B Over-wintered stubbles, followed by an undersown spring cereal and a grass ley
Option 3: Crop margins with no summer insecticide
3A Conservation headlands
3B Conservation headlands with no fertiliser applications
Option 4: Field margins and strips
4A Grass field margins by natural regeneration or sown grasses
4B Beetle banks
4C Uncropped wildlife strips
Option 5: Wildlife seed mixtures

1.2.1 Option 1B: Over-wintered cereal or linseed stubbles, followed by spring/summer fallow.

This option was specifically designed to provide breeding habitat for Lapwings and also Stone Curlews *Burhinus oedicnemus* in the East Anglia pilot area, with potential benefits for spring germinating arable plants.

After the crop (cereal or linseed) is harvested a set of conditions are stipulated for the management of the stubble:

i) Straw from the previous crop must be removed immediately after harvest

ii) No burning of crop residues is allowed

iii) No sub-soiling, ploughing or cultivation of the agreement land

iv) No sowing of a cover crop, and no cutting, topping or grazing of regenerating vegetation

v) No application of agrochemicals (except from a limited selection outlined in MAFF (1998), or with agreement of the relevant MAFF Project Officer).

vi) No applications of organic or inorganic fertilisers, or liming materials.

Fallow establishment and subsequent management have to meet the following restrictions and deadlines:

i) A false seedbed must be created by cultivating the soil between 1st March and 20th March. This must be done with a tractor mounted tined or disc implement to a depth of 75-100mm. Further cultivation is not allowed until 15th July.

ii) No cutting, topping or grazing of the regenerating vegetation

iii) No application of agrochemicals (see above)

vii) No applications of organic or inorganic fertilisers, or liming materials.

iv) After the spring cultivation there should be no mechanical operations on the land before 15th July, as these could disturb breeding birds.

After the 15th July, the land is then subject to normal management. The agreement land then moves to another field to follow a cereal or linseed crop.

1.3 STUDY SITE SELECTION

The Arable Stewardship Scheme pilot area in Shropshire was the core study area for the full duration of the project over two breeding seasons 1999-2000. In 1999 only, a similar investigation of breeding Lapwings was undertaken in the Cambridge Arable Stewardship pilot area by the RSPB. Where appropriate some of these data were incorporated with the core study area data, especially in light of the loss of the 2001 field season due to the outbreak of foot and mouth disease, which curtailed all fieldwork for that year.

1.3.1 Shropshire

All study farms that were selected were within the Arable Stewardship Scheme pilot area (Figure 1.4). Initial enquiries were made to the relevant County Bird Recorder for information where breeding Lapwings had been recorded in the previous five years. Raw data were made available from the 1998 BTO/RSPB Lapwing survey, from which four tetrads out of thirteen were occupied. Arable Stewardship Project Officers were contacted for information regarding farm holdings that had Option 1B incorporated into their agreements. These farmers were contacted to enquire about the presence of Lapwings on their respective farms and surrounding areas. With the information from the above sources, initial surveys were conducted to identify suitable study sites. In 1999, nine farms with Arable Stewardship agreements (and Option 1B) and 11 farms without agreements were selected for intensive study. For the 2000 field season, two additional fieldworkers were employed on the project to undertake fieldwork which allowed the expansion of study sites. New sites selected in 2000 were predominantly new agreement farms that had the Option 1B prescription.

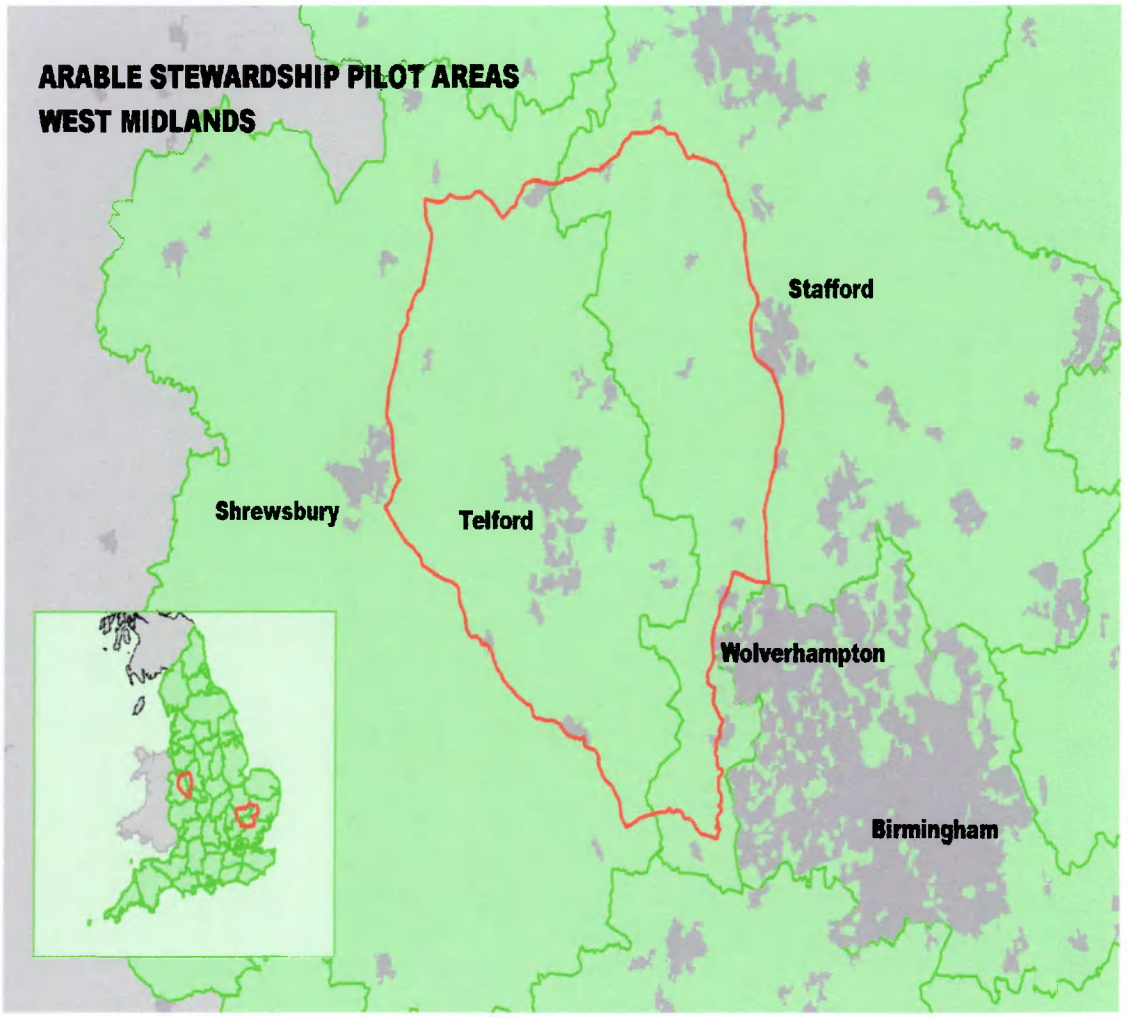

Figure 1.4. The Arable Stewardship Pilot Area in the West Midlands Region (Source: map provided by Andrew Sherrott, DEFRA).

1.3.2 Cambridge

As with the Shropshire study area all study farms were selected from within the Arable Stewardship pilot area (Figure 1.5). Initial inquiries were made to the relevant County Bird Recorders, along with reference to the data from the 1998 BTO/RSPB Lapwing survey and 1998 Cambridge Bird Club survey of breeding Lapwings. The national survey found only one out of 28 tetrads surveyed to be occupied by breeding Lapwings (A. Wilson, *pers.comm.*), and the Cambridge bird survey found breeding birds in 13 out of 75 surveyed tetrads (Pollard & Radford, 1998). Due to time constraints and to minimise travel distances it was decided to concentrate efforts within the Newmarket, Cambridge, and Royston area. From the above enquiries this area was known to hold reasonable numbers of breeding Lapwings in 1998.

Systematic searches of the area were made to identify specific land holdings that had Lapwings exhibiting breeding behaviour. A total of 11 sites were chosen for study, nine were located by early April, and two further sites were subsequently identified by mid May. Of these, five of the farms had been entered into Arable Stewardship agreements. Due to the low density of both the study species and the specific 'Lapwing option,' there was no specific targeting of research effort directed at Lapwings breeding on the Option 1B prescription. Instead an assessment of the breeding ecology of the species in the wider arable landscape was made.

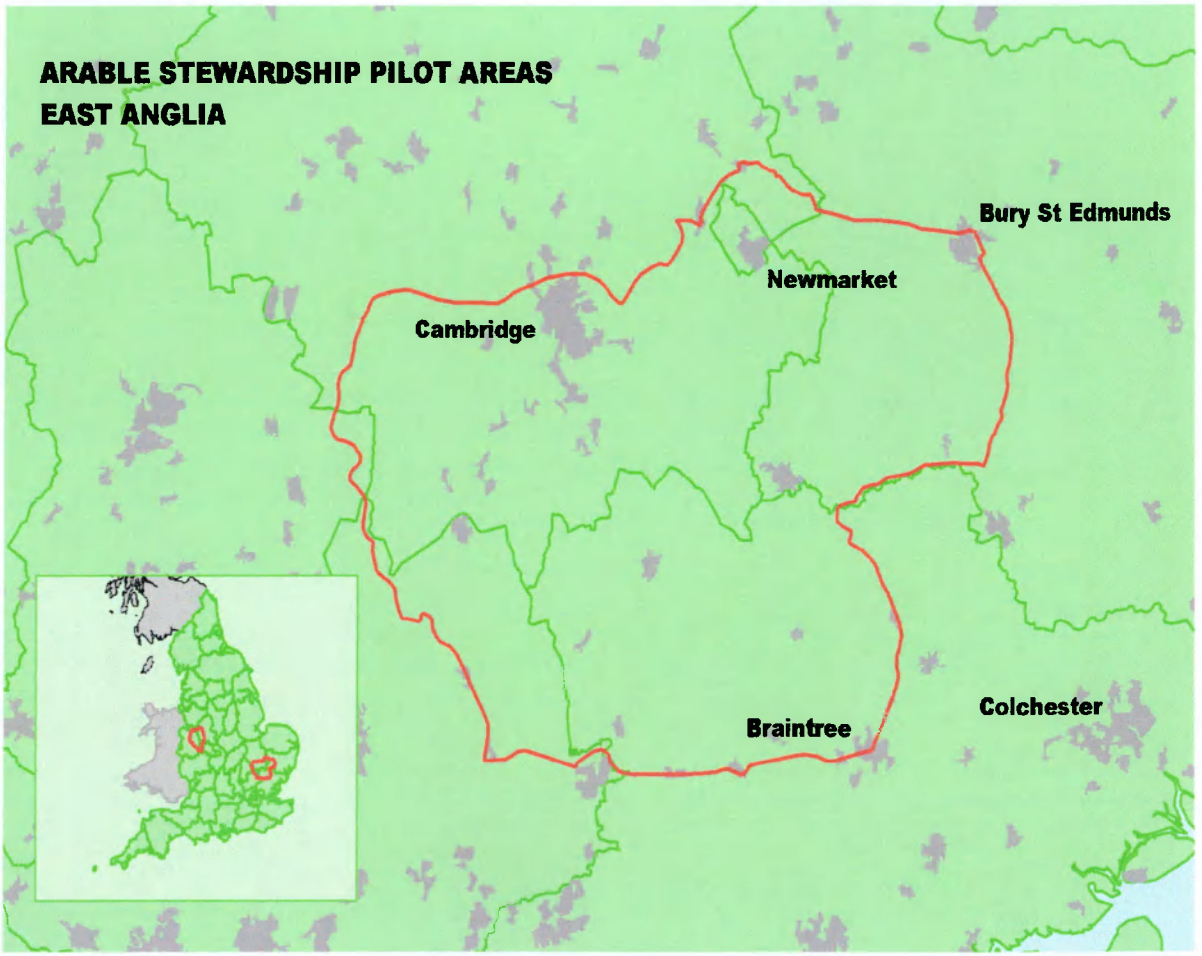

Figure 1.5. The Arable Stewardship Pilot Area in the East Anglia Region (Source: map provided by Will Foss, DEFRA)

1.4 THESIS AIMS AND STRUCTURE

1.4.1 Aims

The project had two broad aims that were interlinked.

Firstly, by the intensive study of a localised population of Lapwings it was aimed to assess the factors that influenced Lapwing breeding ecology, including the nesting and chick rearing phase of the breeding cycle, within an arable landscape.

Secondly, an assessment of the Arable Stewardship Option 1B prescription was made, to determine if there were any potential benefits that may enhance Lapwing breeding success, and where appropriate to suggest improvements to the prescription.

1.4.2 Hypothesis

By providing suitable breeding habitat conditions for Lapwings, both nest and chick survival can be enhanced, which could have positive benefits for Lapwing populations breeding within arable landscapes.

1.4.3 Thesis structure

This thesis has been structured so that each chapter has a common theme, each being readable on its own. To avoid repetition of methods where they are repeated in subsequent chapters, the reader is referred to the chapter where that particular method was initially mentioned. Similarly, the references for each chapter are amalgamated into one reference section at the end of the thesis, to prevent repetition of a number of key references.

CHAPTER 2

CLUTCH INITIATION DATES, CLUTCH CHARACTERISTICS AND HATCHING RATES

2.1 INTRODUCTION

It is clear from analysis of ringing data (Peach *et al.*, 1994; Catchpole *et al.*, 1999) that the Lapwing population decline recorded in England and Wales (Wilson *et al.*, 2001) is being driven by demographic changes associated with the breeding season. Lapwing productivity during the breeding season is ultimately dependent on i) nesting stage factors: clutch characteristics (this chapter), nest survival (chapter 4), and ii) mechanisms influencing chick survival and fledging rates (chapter 5). Any changes in one (or more) of these parameters must be compensated by a corresponding change in another if the population is to remain stable.

Egg laying by Lapwing can start as early as mid March, but the peak period for nesting is early to mid April (Galbraith, 1988a; Hegyi, 1996; Shrubb, 1990). As spring crops are the favoured nesting habitat for Lapwings, nest loss can be high if cultivations and egg laying coincide.

In common with most Holarctic waders, Lapwings lay determinant clutches of four eggs (Arnold, 1999). Variation in clutch size is indicative of environmental conditions, and the optimal clutch size for an individual is larger when conditions are most favourable (Perrins, 1965). Given that Lapwings are able to produce five eggs if the first is removed (Klomp, 1970), and are able to lay many replacement clutches in a season, clutch size does not appear to be constrained by egg formation costs, and four eggs would appear to be the optimum clutch size for this species. However, the reverse of this is that Lapwing clutches should be smaller if modern agricultural landscapes are a poor quality habitat, and if agricultural change was affecting the ability of Lapwings to produce eggs. A review by Arnold (1999) suggests that the upper limit on Lapwing clutch size is best described by the incubation-limitation hypothesis, in that the maximum number of eggs is set at four due to the physiological inability to incubate more eggs. Therefore, any changes to the number of eggs being laid by Lapwings will only be apparent if environmental effects are manifesting themselves through a reduction in clutch size.

Alternatively, variation in clutch investment maybe reflected in individual egg volume, with better quality habitats having positive benefits for Lapwing maternal condition with a subsequent fitness premium on laying larger eggs (Redmond, 1986; Galbraith, 1988b; Grant, 1991). Individual egg investment is partly dependent on maternal condition (Högstedt, 1981, Olsen *et al.,* 1994) and it has been shown in Lapwings that maternal mass and condition are positively correlated with egg volume (Galbraith, 1988b; Blomqvist & Johansson, 1995). Factors affecting maternal body condition at the breeding site include extrinsic factors, such as food availability, which are likely to be strongly influenced by agronomic practice. Intrinsic factors, such as innate individual differences, are likely to influence body condition but are beyond the scope of this work. Adult Lapwing are less able to influence chick quality post-hatching as the chicks are self-feeding (altricial parents can maximise food provisioning rates), and as such parental investment in egg quality assumes more importance. The ability to invest in egg quality must be somewhat dependent on the available food supply during the prelaying period, as well as stored reserves, hence habitat quality might exert an indirect effect on egg investment. In both altricial and precocial species, chicks hatched from large eggs are heavier and larger than those from smaller eggs (Parsons, 1970; Grant, 1991) and this has been demonstrated in Lapwings (Galbraith, 1988b; Hegyi, 1996; Linsley, 1999; this study Chapter 5), with a subsequent positive effect on chick survival (Galbraith, 1988b). Although there are likely to be selective pressures opposing increased egg volume, with adults that lay smaller eggs able to lay earlier (Furness, 1983) which may coincide with peak food availability.

Intra-clutch egg-mass variation could result from nutritional constraints on the laying female (Järvinen & Ylimaunu, 1986). For example, laying females in poor physiological condition, such as those with low body reserves, would lay fewer eggs or clutches with higher variation in egg mass. Nutritional constraints on egg size may be important in species that acquire resources for egg formation prior to and during the laying period (Viñuela, 1997), as in shorebirds (Erckmann, 1983); and as highlighted in Lapwings (Högstedt, 1974). Constraints may be especially applicable to cases where egg mass declines with laying sequence, since the relative mass of last-laid eggs would

depend on the degree of depletion of reserves (this has not been documented in Lapwings). However, the factor limiting egg size need not be energy but some other nutritional constraint imposed by the laying process. For example, minerals or proteins are required in large amounts to form eggs, and limitations may constrain egg formation (Rickleffs, 1974).

Koenig (1982) suggested that hatching rates were related in part to diet and nest site. If agricultural practice is responsible for declines in food availability and modern cropping practice responsible for poorer quality habitat, negative effects on hatching rates may be expected. In domestic fowl, hatching rates are positively correlated with nutrition (Taylor, 1949) and so may be an indirect indicator of food availability or maternal body condition in wild bird species. The failure of an egg to hatch represents a serious loss of energetic input and reproductive output by individual females (Koenig, 1982). As clutch size in Lapwings appears constrained to four eggs, any reduction in hatching rates are likely to be influenced by extrinsic factors rather than increased metabolic demands on the female (Thomson *et al.*, 1998). With an increase in chemical inputs over the last 20 years (Chamberlain *et al.*, 2000) hatching rates may be expected to be affected by pesticide application. Long term nest record data for corn bunting *Miliaria calandra* demonstrate increased productivity following the cessation of organochlorine use (Crick, 1997). The high incidence of egg sterility amongst some American farmland birds has been associated with the effects of pesticide contamination (Long, 1963). Conversely, Donald *et al.*, (2001) could find no differences between intensively managed cereals and unmanaged set-aside, suggesting that there are no effects of agro-chemicals on the hatching rates of skylarks. Similarly, Odderskær *et al.*, (1997a) detected no difference in hatching rates (of skylarks) between sprayed and unsprayed cereal fields.

This chapter aims to:

i) assess agricultural variables that may influence clutch size, egg volume and hatching rates,

ii) to identify temporal patterns in nest initiation dates,

iii) to identify how all these may affect Lapwing productivity at the clutch level.

2.2 METHODS

2.2.1 Data collection

Nest data were collected from the Shropshire study area in 1999 and 2000, and from the Cambridge area in 1999 only. Nests were located by the presence of territorial adult birds and the observation of incubating females. Although there is little evidence to suggest that nest marking can influence breeding success (Galbraith, 1987), a precautionary approach was adopted, and the use of existing landscape features combined with a measured number of paces on a specific bearing was used in nest relocation. When a nest was first located the clutch size was recorded and all eggs were weighed using an electronic balance to 0.1g and individual egg length and breadth was measured using dial calipers to 0.1mm.

The date on which the first egg of a clutch was laid and expected hatching dates were estimated by one of two methods:

a) If a clutch was found prior to the last egg being laid, the first egg and clutch completion dates were calculated on the assumption that the laying interval between successive eggs was 2 days (Galbraith, 1988a). The expected hatching date of each clutch was estimated as 25 days after clutch completion (Galbraith, 1988a).

b) Most nests were found after clutch completion, and the first egg date and expected hatching dates were estimated from the mean egg density:

$$\text{mean egg weight/mean egg volume (obtained from length} \times \text{breadth}^2 \times 0.457)$$

Expected hatch dates could then be estimated using a predictive equation developed by Galbraith, (1988a):

days till hatching=150.84density-140.68 (r=0.905, P=<0.001), mean error of 2.3 days (s.d.=1.876).

Once the hatch date of each clutch of unknown age had been estimated, the first egg date was back calculated using the same criteria as described above.

Nests were checked at intervals (every 4-10 days) to obtain data on breeding success and timing of hatching, with the time between nest visits decreasing nearer to expected hatching dates. Chicks were usually located in the nest scrape, and hence the number of successful/unsuccessful eggs could be determined. Complete clutch abandonment was not analysed here (13 out of a total of 238 (5%) nests were abandoned) but this will be investigated in Chapter 4.

Soil moisture deficit (SMD) was determined using an irrigation scheduling software package (IMS, environmental software, ©Cranfield University, 1995) in conjunction with climatological data provided by Harper Adams University College weather station, 52° 46′ N 2° 25′ W (Shropshire study area), and Royston Weather Station, 52° 03′ N 0° 0′ W (Cambridge study area). SMD data were crop specific (Appendices 2 and 3), however, each daily reading per crop type was combined and divided by the number of crop categories to give an additional daily average SMD reading for each area. Both crop specific and average SMD data were incorporated in to the analyses.

2.2.2 Data analysis

Analysis of clutch size was limited to nests that fulfilled one of two criteria, i) those nests in which consecutive observations of more than 2 days apart showed the same number of eggs to be present, or ii) if 4 eggs were recorded on the first visit and was subsequently observed to be lower then the clutch size was deemed to be 4 (only 2 nests out of 185 were recorded with more than 4 eggs).

First egg dates were calculated as the number of days since January 1st (for example, 30 April= day 120) and were plotted graphically to identify temporal patterns.

2.2.2.1 *Clutch size and egg volume*

A multivariate analysis with categorical and continuous variables was undertaken. GLIM 3.77 was used to model clutch size using normal errors and an identity link (Crawley, 1993). A dataset (n=225) was used incorporating data from the Cambridge study area in 1999, using the explanatory variables first egg date, and a crop specific and an average daily soil moisture deficit in a 10 day period prior to the first egg. The following categorical variables were also used, crop category (7-level), region (2 level), and nest status (2 level, indicating whether the nest was a first nest or a replacement nest). Soil moisture deficit is an indicator of the amount of water within the soil, which has been shown to positively affect earthworm abundance in the upper soil. Högstedt (1974) shows that earthworm abundance has a positive affect on egg formation periods. Mean egg volume was modelled using the same rationale (n=190), with clutch size incorporated as an explanatory variable. The maximal model was fitted to each dataset and all explanatory variables were deleted in turn to assess the significance of the term in respect to the reduction in deviance. The variable explaining the least amount of deviance was dropped if it was non-significant. This process was repeated until the only terms left in the model were significant. The goodness of fit of the final models was assessed by plotting standardised residuals against the standard normal cumulative distribution function using the MCHECK macro in Crawley (1993). As many nests were found within the same farm, potential problems arise associated with spatial autocorrelation. To test for this, a categorical farm term was entered into all minimum adequate models (MAMs), a significant reduction in residual deviance would indicate the presence of farm level spatial autocorrelation.

2.2.2.2 *Intra-clutch variation*

Intra-clutch egg size variation was investigated by determining an egg symmetry index which was considered as the degree to which each egg was similar to the others in the clutch (Kilpi, 1995; Catry & Furness, 1997). To calculate this, eggs within clutches were ranked in order of size and the relative size of each egg was calculated with respect to each other egg by dividing the volume of the

smaller egg by the volume of the larger one in each comparison (Amat *et al.*, 2001). These calculations were undertaken for every pair of eggs in the clutch, so that six values were obtained for each nest (four egg clutches only), which were then averaged. This egg symmetry index was then treated as the response variable. GLIM 3.77 was used to model egg symmetry using normal errors and an identity link (Crawley, 1993). The categorical explanatory variables year (2 level), farm (11 level), crop (7 level) and nest status (first or replacement) and the continuous variables clutch volume and first egg date were all entered into a maximal model. The same deletion procedure outlined above to model clutch size was followed. Only the Shropshire data (both years) was used in the analysis of intra-clutch variation.

2.2.2.3 *Hatching rates*

Hatching rates were modelled using a binary response variable, where unhatched eggs were present or absent once incubation was completed and at least one chick hatched from the clutch. A binomial error structure was declared and a logit link function adopted (Crawley, 1993). The explanatory variables incorporated into maximal models were first egg date, crop category, average egg volume and nest status. A change in deviance caused by removing an explanatory variable from the maximal model was treated as a likelihood ratio test and compared with the χ^2 distribution with the appropriate degrees of freedom to assess its significance. The deletion procedure as outlined above was adopted.

2.3 RESULTS

A total of 225 nests were located over the 2 years of the study, 99 nests in 1999 (46 in Cambridge and 53 in Shropshire), and 126 nests in 2000 in Shropshire. As there was no difference in the frequency distribution of clutch size between years (χ^2=1.17, 1 d.f. n.s. Yates correction applied), all data was combined into one dataset. The distribution of nests by crop category in relation to clutch size is given in Table 2.1.

The earliest initiated nest was recorded on 16 March (Cambridge 1999) and the latest on 3 June (Shropshire 2000), with the peak initiation period being between 26 March and 19 April (Figure 2.1).

Table 2.1. Frequency distribution of clutch size (percentage in parentheses) by crop type.

	Clutch size				Total
	2	3	4	5	
Winter crops	-	5 (17%)	25 (83%)	-	30
Option 1B	1 (3%)	5 (13%)	33 (85%)	-	39
Spring cereal	1 (3%)	4 (11%)	31 (86%)	-	36
Grass	-	2 (17%)	10 (83%)	-	12
Set-aside	3 (7%)	5 (12%)	32 (78%)	1 (2%)	41
Stubbles	1 (6%)	4 (24%)	12 (71%)	-	17
Other spring crops	1 (2%)	6 (12%)	42 (84%)	1 (2%)	50
TOTAL	7 (3%)	31 (14%)	185 (82%)	2 (<1%)	225

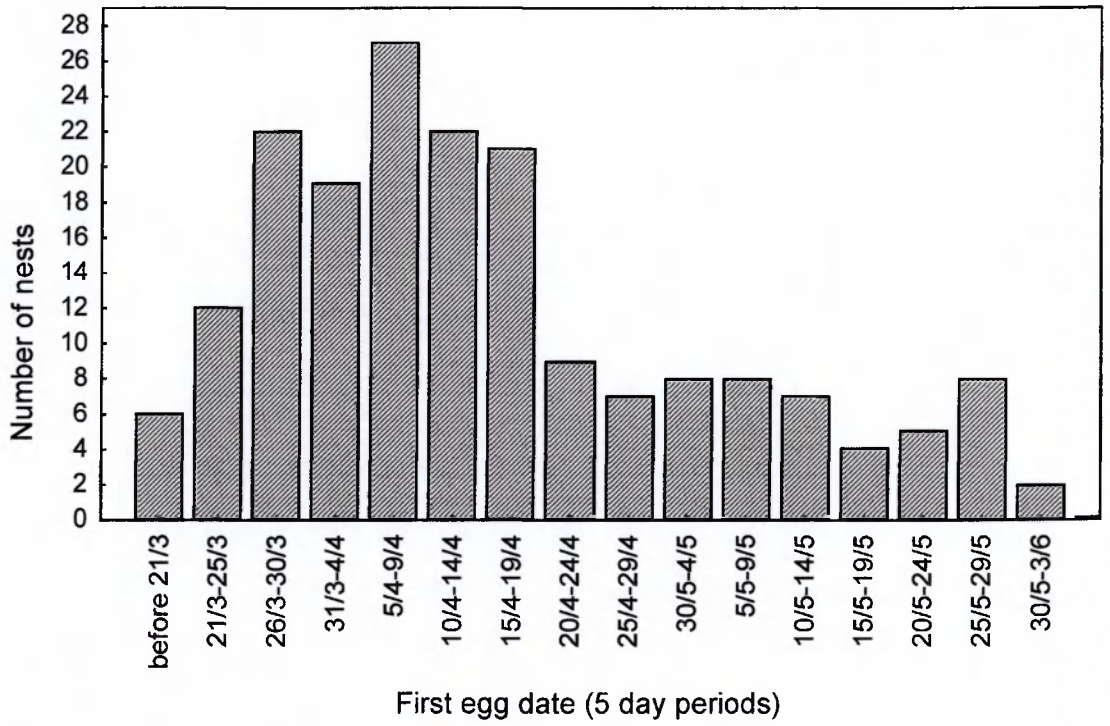

Figure 2.1. Distribution of Lapwing nest initiation dates by 5 day periods. The peak nesting period is the first week in April, with the 'tail' of nests in May and June representing replacement clutches.

2.3.1 Clutch size

Mean clutch size was 3.81 (s.d.=0.49), with a modal average of 4. The categorical variable region was retained in the minimal model ($F_{1, 223}$=3.94, P=<0.05), and clutch size differences between the two regions are explained by the greater proportion of 4 egg clutches in Cambridgeshire (Table 2.2). There was no evidence for spatial autocorrelation as the farm term was not significant when added to the MAM ($F_{13, 210}$=0.79, n.s.). There was no significant difference in clutch size between crop types ($F_{6, 218}$=0.29, n.s.) and there was no evidence that clutch size varied as the breeding season progressed ($F_{1, 223}$=0.55, n.s.). Similarly, all other explanatory variables were deleted from the maximal model without any significant reduction in deviance.

Table 2.2. Clutch frequency differences between regions. A categorical regional term was retained in a minimal model ($F_{1, 223}$=3.94, P=<0.05). Note the greater proportion of 4 egg clutches in Cambridgeshire.

	Clutch size				
	2	3	4	5	mean
Shropshire	6	30	141	2	3.78
Cambridgeshire	1	1	44	-	3.93

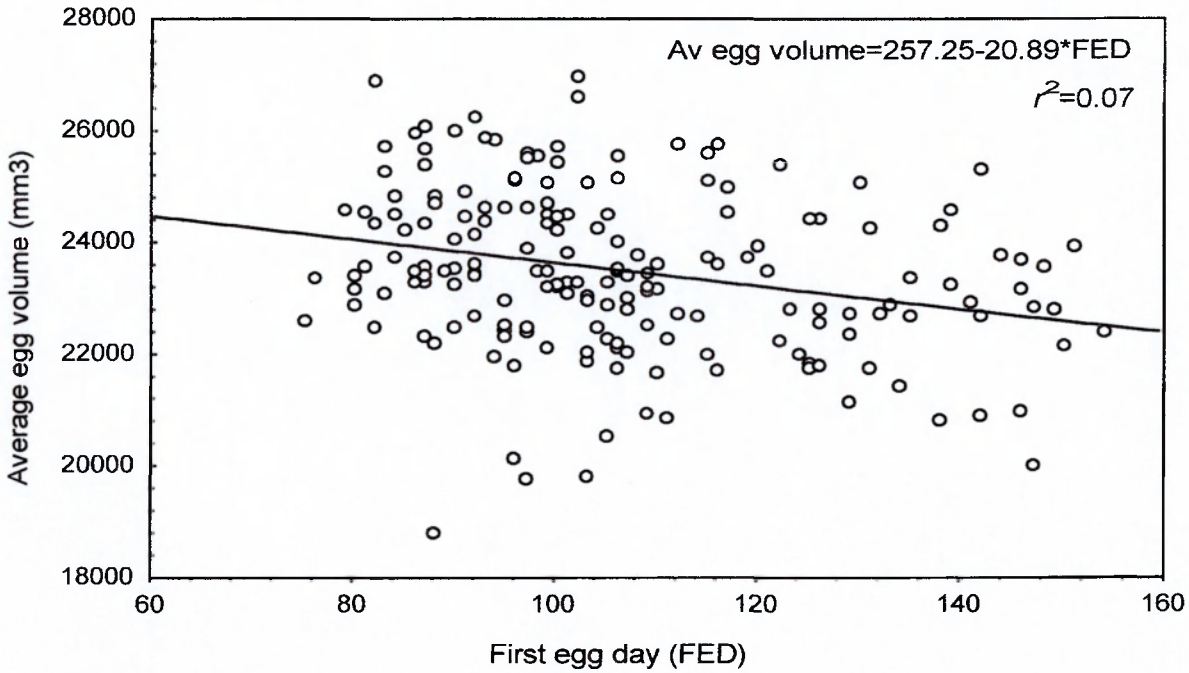

Figure 2.2. Relationship between nest initiation date and average egg volume. Where day 120=30 April.

2.3.2 Egg volume

The single explanatory variable retained in the maximal model was first egg date ($F_{1, 189}$=13.43, P<0.01), although the explanatory power of the model is weak r^2= 0.07 (Figure 2.2). All other terms were deleted from the maximal model, including the farm term, without any significant reduction in deviance.

2.3.3 Hatching rates

A sample size of 124 nests (Shropshire data only) were used to investigate hatching rates from which 23 nests (18.5%) contained at least one egg that failed to hatch. Of these, 18 nests (78.3%) had one unhatched egg, 4 nests (17.4%) had two unhatched eggs, and 1 nest (4.3%) had 3 unhatched eggs. All explanatory variables were deleted from the maximal model. A reduced sample size (116 nests) incorporating average egg volume as an explanatory variable showed no effect upon the occurrence of unhatched eggs in the nest ($F_{1, 114}$=0.45, n.s.).

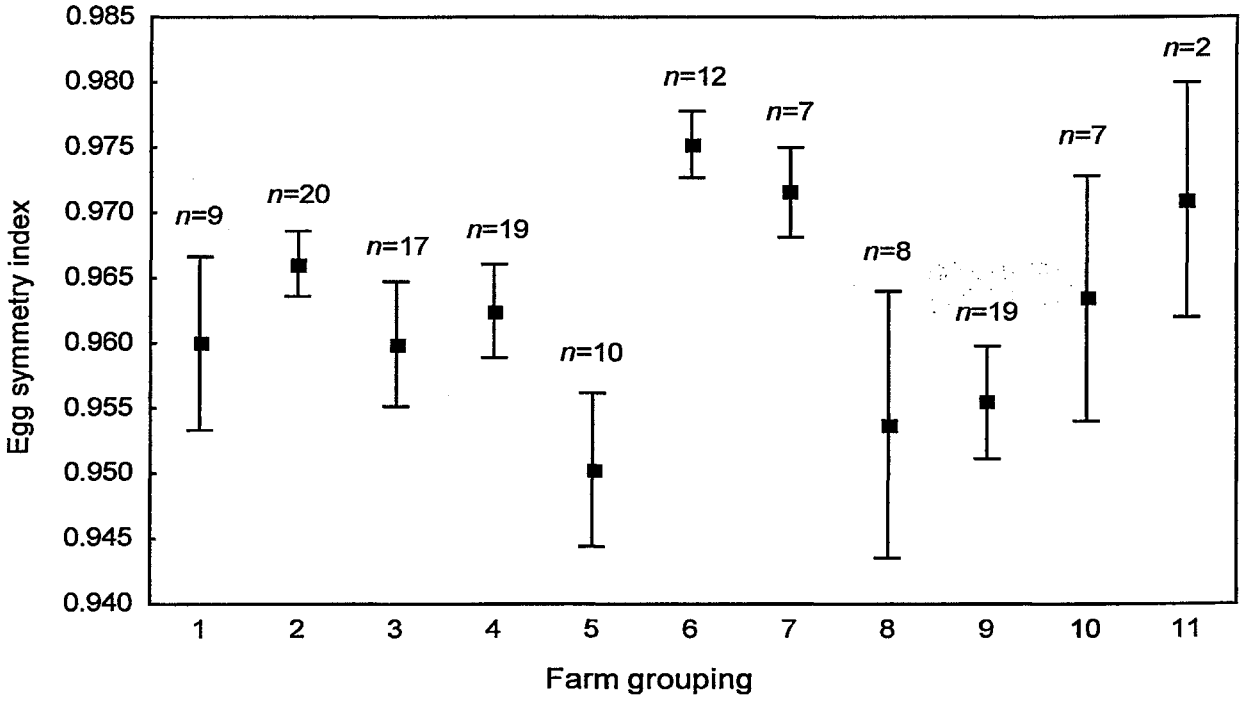

Figure 2.3. Mean egg symmetry indices by farm grouping. Mean with one standard error is shown. See Appendix 3 for explanation of farm groupings.

2.3.4 Intra-clutch variation

The farm variable was retained in the MAM ($F_{10, 119}$=1.972, P=0.042). *Post hoc* testing (Tukey test) shows that the only 2 farm categories that differed were 5 & 6 (P=0.046), (Figure 2.3). Farms in category 5 had larger fields (7.6ha), more winter crops (26% of cropped area) and fewer Arable Stewardship agreement holders (1 out of 5), than category 6 farms (field size=5.9ha, 10% winter crops and 2 out of 2 Arable Stewardship agreement holders), (see Appendix 3). All other explanatory variables were deleted from the maximal model. However, the categorical variable crop type approached significance ($F_{6, 123}$=2.05, P=0.064) (Figure 2.4).

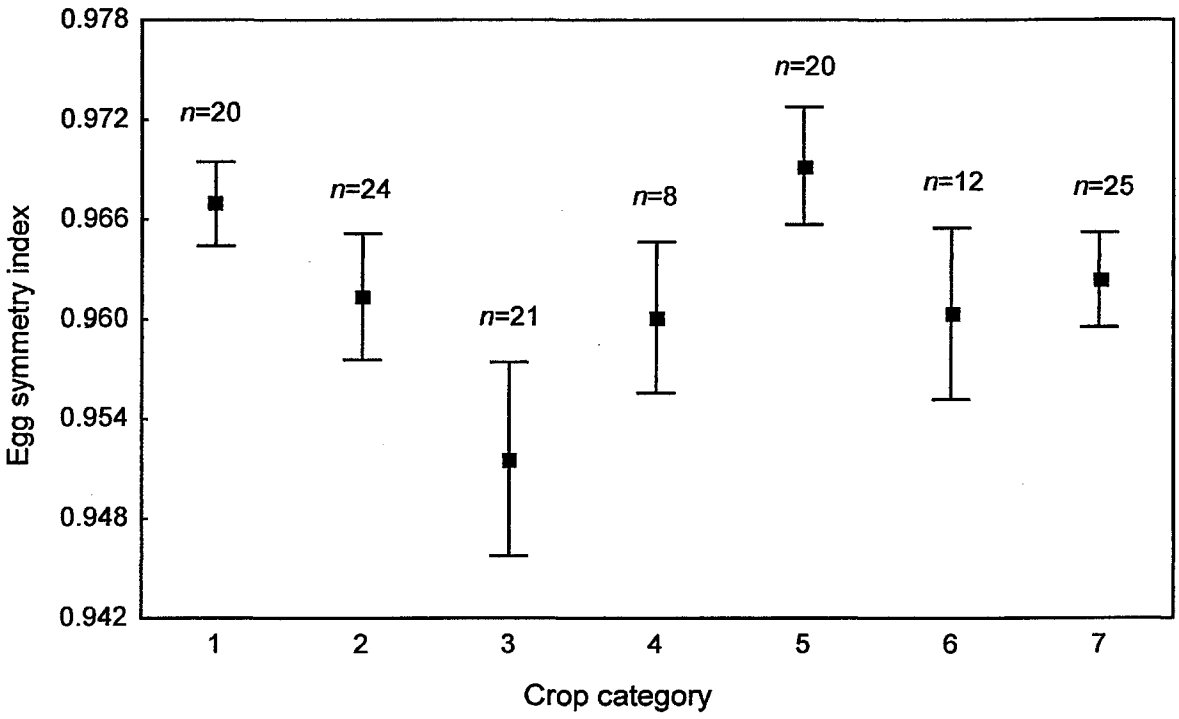

Figure 2.4. Mean egg symmetry indices by crop category. Mean with one standard error is shown. Where 1=winter crops, 2=Option 1B, 3=spring cereal, 4=grass, 5=set-aside, 6=all stubbles, and 7=other spring crops.

2.4 DISCUSSION

The distribution of first egg dates of Lapwing clutches is similar to other published studies (Galbraith, 1988a), with a peak of nesting activity around the end of March to early April, and a subsequent 'tailing off' of nests which almost certainly represents replacement clutches. Although without a marked population of adults it is uncertain whether these are genuine replacement clutches or poor quality later breeders. The former is most likely as Lapwings are known to lay subsequent clutches after initial clutch failure (Klomp, 1951). The cessation of nesting by the first week in June is likely to be due to constraints on habitat availability rather than any physiological limitation of the species. This was highlighted by Galbraith (1988a) who noted that nesting birds in late May were on fields that had been ploughed and drilled later than usual due to adverse weather conditions, all crops in other fields were 20-30cm in height. Furthermore, he noted that at least two or three of the late clutches were laid by females that had ceased breeding and joined post-breeding flocks, only nesting when new suitable habitat became available. In addition, on grassland sites on the Ouse Washes nesting in 1998 extended in to mid June, although this year was characterised by flooding during the peak breeding season (Tyler, *Unpublished data*). However, there is likely to be a trade-off between late breeding and the reduction of food availability as the breeding season progresses. Adaptive pressure to breed early in Lapwings to coincide with maximum food availability within arable habitats may limit the likelihood of late nesting. A change in breeding phenology of Lapwings (and other 'meadow birds') has been shown in Holland (Beintema *et al.*, 1985) where agricultural changes via increased fertiliser inputs and earlier mowing has led to an evolutionary response of earlier breeding. Changes in drilling dates and crop growth rates for spring cereals are largely dependent on weather and have probably remained fairly stable in the last 20 years, and consequently it seems that such an adaptive response in breeding phenology for arable nesting Lapwings is unlikely. Earlier spring drilling dates, such as February, are likely to have positive benefits in terms of nest survival, but may lead to a reduction in food availability (see Chapter 6),

which may have consequences for egg quality. Conversely, in years of high rainfall, the delaying of drilling may well coincide with the onset of the laying period, and nest losses could be high, with a large number of subsequent replacement clutches (which may have knock-on effects on both nest and chick survival). The cultivation dates (between the 1st and 20th March) stipulated by the Option 1B prescription would appear to be ideal in terms of limiting nest loss through agricultural operations. Only six nests in two years were initiated prior to the 21st March.

Analysis of nest record cards between 1962-1985 showed that there has been no change in mean clutch size in arable habitats over time (Shrubb, 1990). The mean figure from this study (3.81) compares favourably with Shrubb's analysis (3.78), and furthermore the difference between mean clutch size between this study and other studies reviewed is no more than 0.2 (Table 1.7). Mean clutch sizes given in Spencer (1953) of 3.85 would suggest that clutch size has remained stable over the last 50 years. However, the most recent analysis of nest record cards, covering the period 1962-99, suggests that clutch size has significantly increased from an average of 3.61 to 3.77. This pattern has been observed in a number of declining farmland birds (Siriwardena *et al.*, 2000), and may arise due to a density dependent response or because only the best habitats are occupied and/or only the 'highest quality' birds are able to breed. Although the upper limit of Lapwing clutch size is highly likely to be set at four in accordance to the incubation limitation hypothesis as proposed by Arnold (1999), that clutch size has not declined in the species would suggest that changes in food supply within agricultural landscapes have not affected the Lapwings ability to lay the optimal clutch size. Alternatively, that there were no significant correlates of clutch size may suggest that the genetic predispostion of Lapwings to lay four eggs is more important than environmental variables. However, if recent documented declines in food resources (Campbell *et al.*, 1997; Wilson *et al.* 1999) continue within agricultural landscapes, this may well lead to an attainment of a threshold level of nutritional availability that may have future repercussions for Lapwing clutch size (and quality).

Galbraith (1988a) and Shrubb (1990) showed that on tilled land clutches were larger on emerged crops than on bare land attributing the difference to loss of incomplete clutches during the cultivation process, followed by incubation of the resulting partial clutch. However, in this study there was no apparent difference in clutch size between spring cultivated crops and winter sown crops. Nests on stubble fields had a lower proportion of four clutch nests than other crop categories and this could be partly explained by an observed protracted cultivation period on some maize stubble fields, which led to a high number of partial clutch losses. The difference in clutch size between regions (Table 2.2) may be similarly explained as few nests were lost in the Cambridge study area to agricultural operations (2 out of 49), and it is apparent that (in Cambridge) the main spring cultivation period does not coincide with the peak nesting period.

Given the clutch size conservatism of the Lapwing, variation in clutch investment may manifest itself through differences in egg size/volume. A relationship between mean egg volume and laying date is apparent. Grønstøl (1997) found a similar relationship between average egg volume and laying date, but when the effect of the females mating status was controlled for this temporal relationship was no longer significant. This suggests that the lower egg volumes of later laying were associated with secondary females. In this study, the mating status of adults were not determined, although from personal observation, it seems that monogamy was the dominant mating system, suggesting a real effect of laying date on egg volume. Both Galbraith (1988a) and Blomqvist & Johannson (1995) found no difference in egg volume between first clutches and replacement clutches, which they attribute to the availability of good quality foraging habitats nearby, Galbraith's study site was a mix of arable, rough grazing and improved pasture where food densities were high. In Blomqvist & Johannson's study female Lapwings foraged mainly on arable fields where the intake of earthworms were high and also mudflats with the presence of large polychaete worms. The availability of earthworms probably has an important influence on Lapwing breeding condition (Högstedt, 1974; Galbraith, 1989a; Baines, 1990), and may well exert a strong influence on energetic input by females in terms of egg quality and size.

The presence of good quality pasture for foraging is likely to be a limiting factor within our study, and the decline in earthworm abundance over the length of the breeding season is a possible explanation for declining egg size (Chapter 5). However, other explanations can not be ruled out, heavier eggs laid early on may be an indicator of 'good' females, with the later clutches being laid by 'poorer' females which would imply that the decline in egg volume is related to genotypic variation as opposed to environmental constraints. Blomqvist & Johansson (1995) found that differences among females were the main source of variation in egg size.

That there is no relationship between crop categories and clutch volume, despite big differences in earthworm biomass (Chapter 5), is probably not surprising given that during the pre-breeding period female Lapwings are not strongly tied to breeding fields but are able to forage in prey rich habitats such as pasture if available.

Differences in egg size within clutches of Lapwings are likely to be influenced by the availability of nutrients and energy during egg formation (Högstedt, 1974), particularly as Charadridae acquire nutrients and energy for egg-laying just before and during egg-laying (Erckmann, 1983). That the farm variable was retained in the MAM would suggest that something about certain farms may be having an effect on the Lapwings ability to acquire sufficient energy and/or nutrients needed during the egg formation period. Basic data on farm characteristics suggest that the farm grouping with the greatest degree of variation within the clutch has the largest field size and a greater amount of the cropped land in winter cropping, both of which are often seen as measures of agricultural intensification. The lack of any significant effect of crop type may suggest that any effect on egg size is specific to farm management, such as intensity of management, chemical inputs, or factors such as underlying soil types. It should be noted that in winter cereals (often seen as indicator of intensification) the egg symmetry index was the second highest after Option 1B. A larger, more detailed data-set is required to elucidate any effect that specific farm management practices may have on egg formation and intra-clutch variation.

There were no detectable differences in hatching rates in relation to any of the explanatory variables used in this analysis. A lack of effect of crop type on hatching rates would suggest that crop specific management does not have any measurable affect on egg viability. The frequency of unhatched eggs in unsprayed habitats (set-aside and Option 1B) was no different when compared to cropped fields, which were highly likely to have received pesticide applications, suggesting there is no detectable effect of pesticide application on hatching rates. Similar results have been found for skylark where hatching rates were found not to differ between intensively managed cereals and unmanaged set-aside (Donald *et al.,* 2001), and also in Denmark where there was no significant difference in hatching rates between sprayed and unsprayed cereal fields (Odderskær *et al.*, 1997a). The lack of effect of mean egg volume upon hatching rates would suggest that any deleterious effects of reduced egg size manifest themselves later in the breeding phase ie. through poor chick survival rather than reduced egg viability. Similar results were obtained by Parish *et al.* (2001) where there was no evidence of an effect of egg volume on hatching success.

That there were few detectable significant effects of the measured agricultural variables on clutch size, egg volume, intra-clutch egg size variation or hatching rates would suggest that Lapwing productivity is not limited by clutch characteristics. There appears to have been little change in mean clutch size (Table 1.7), however, whether a reduction in egg quality has occurred is impossible to assess in the absence of long-term data on egg volume. If there has been any changes in clutch 'quality' in recent years they would most likely be in response to poor maternal condition as a consequence of limited food sources- there is no published data to support this.

The key findings of this chapter are

i) the identification, and the timing of, the peak period of nest initiation

ii) the decline in mean egg volume in relation to first egg date

CHAPTER 3

FACTORS AFFECTING NEST-SITE PLACEMENT AT DIFFERENT SPATIAL SCALES

3.1 INTRODUCTION

Nest-site selection involves the specific choice of a site to build a nest, which usually occurs just prior to egg laying (Cody, 1985). Proximate cues in general habitat selection by Lapwings may involve elements of site philopatry, competition, presence and availability of certain landscape features. To understand the population decline of any species there must be a comprehensive understanding of how that particular species utilises the landscape that is available. The comparison of habitat use before and after the population decline can provide preliminary hypotheses aimed at understanding and reversing such declines. Analyses of habitat data and bird surveys at the landscape scale, such as the tetrad scale (2 x 2km) adopted by Wilson *et al.* (2001), have identified habitats within arable landscapes that are associated with the presence or absence of territorial Lapwings. Winter crops are generally avoided and Lapwings show a strong preference for spring tillage, with an increasing preference when spring tillage is abutting grassland. Similarly, Galbraith (1988a) highlighted the importance of the juxtaposition between spring tillage and livestock pasture. Other studies have shown that Lapwings select nest-sites in relation to certain landscape features. Work by Elliot (1982) showed that Lapwings nested significantly further away from trees than would be expected purely by chance, and similarly Berg *et al.* (1992) showed a positive response of nest survival in relation to increased distance from predator perches. In The Netherlands, nesting densities were found to show a negative response to the proximity of roads (Van der Zande *et al.*, 1980), although Milsom *et al.* (2000) found no conclusive evidence to suggest that the presence of footpaths and proximity to roads had an effect on the presence or absence of Lapwings on coastal marshes in Kent, England, during the breeding season. However, the same authors did show that the occupation of marshes were less likely in the presence of National Grid pylons.

In contrast, finer scale, within field nest-site selection is less well understood. On coastal grazing marshes Milsom *et al.* (2000) show that the optimum sward height for Lapwings (at the field level) was between 30-50mm and that occurrence of occasional tussocks was a good predictor of a given field containing a Lapwing territory. Whilst Lapwings are known to prefer nest-sites with short or

no vegetation (Klomp, 1954; Lister, 1964; Kooiker, 1984; Galbraith, 1988a; Berg *et al.*, 1992) there are few quantitative assessments relating to the specific vegetative characteristics that the species require in the immediate vicinity of the nest, particularly within arable fields. Conservation measures aimed at Lapwings, are likely to be implemented at the field level through agri-environment schemes such as Countryside Stewardship and the current Pilot Arable Stewardship Scheme. A better understanding of nest site selection by Lapwings would help increase the effectiveness of such schemes.

The general aims of this chapter are

i) to determine if nest-site selection in relation to vegetative characteristics is a random process or if certain characteristics are being selected,

ii) to identify differences in both vegetative and landscape characteristics associated with Lapwing nests in a variety of crop types, and

iii) to identify common themes at varying spatial scales which can be applied to Lapwing conservation.

3.2 METHODS

3.2.1 Fine-scale data at the nest-site

The specific aim of this section is to identify important sward characteristics that determine the placement of nests within fields, for a variety of crop types.

3.2.1.1 *Baseline ground surface data.*

Data were collected from seven crop types: winter wheat (n=9), winter beans (n=4), spring barley (n=11), sugar beet (n=3), potatoes (n=3), set-aside (n=7) and Option 1B (n=10), where n=fields. The fields were selected prior to the onset of breeding, and did not necessarily have Lapwing territories on them. Furthermore, the cropped fields were selected because they represented typical agronomic qualities that farmers strive for, such as good crop establishment. Ten quadrats ($0.5m^2$) were taken from the central area (a minimum of 50m from the nearest boundary) of the field, each quadrat being thrown in a random direction and distance. The following characteristics were

recorded; percentage crop cover, bare ground, broad-leaved weed cover, grass weed cover, and stubble cover. The number of each of these vegetation components present in each quadrat were recorded on a scale of 1 to 5 to give a diversity score. Using a 1m wooden pole marked with 1cm gradations, five height measurements were taken from each quadrat, one from each corner and one from the centre. This was used to give an average vegetation height for each quadrat. Along two adjacent sides of each quadrat, ground structure measurements were taken to quantify the amount of variability in the surface topography of the ground. A one metre length of wood with ten holes, the centre of each hole being 8cm from the next, was positioned parallel to the side of the quadrat. Through each of the holes was dropped a 20cm long wooden peg marked with 1cm gradations, when the peg made contact with the ground, a reading in centimetres was taken from each of the ten positions. This was repeated for one adjacent side of the quadrat. To quantify the variability of the surface topography the standard deviation of the mean was calculated for the twenty ground structure measurements that were taken for each quadrat.

Repeat measurements were taken two weeks apart, over 5 sampling periods extending from 20th March to 20th June. Winter crops were not monitored during the final sampling period, primarily due to the likelihood of damage to the crop, and spring drilled crops were not measured during the first sampling round as many cultivations had not been completed. The sampling procedure described above was used for each of the sampling rounds, with the exception of ground surface topography measurements which were taken on the first sampling round only. It was unlikely that surface topography altered significantly once cultivations had been completed.

3.2.1.2 *Ground surface data at the nest-site*

Lapwings lay a clutch of 2 to 5 eggs (modal average of 4) in a shallow scrape on the ground, with a rudimentary nest lining of vegetation (Cramp & Simmons, 1983). Nests were located by observing incubating females. Once the nesting attempt had been identified the nest was visited to record egg biometrics, crop characteristics and ground structure. First egg dates and hatching dates were estimated using the procedure outlined by Galbraith (1988a) (see Section 2.2.1). A quadrat was placed over the nest, with the nest scrape being at the centrepoint, and measurements were

taken using the methodology described in section 3.2.1.1, with the exception that the central vegetation height measurement was taken adjacent to the nest scrape. This process was then repeated for four quadrats abutting the nest scrape quadrat in a north, south, east and west direction. To keep nest disturbance to a minimum, ground topography measurements were only taken from the quadrat north and south of the nest scrape. Similarly, during periods of heavy rainfall ground topography measurements were not taken to prevent obvious footprints being left around the nest. Within the nesting field, measurements from a further ten random quadrats were taken using the same procedure. These random measurements were taken at least 50m away from the nest scrape and field boundaries.

Across all crop categories, nest site data were recorded for 99 nests, winter cereals (n=15), winter beans (n=6), spring cereals (n=22), other spring crops (n=20), stubbles (n=11), set-aside (n=13) and Option 1B (n=12). Ground topography measurements were taken at 61 nests, winter cereals (n=8), spring cereals (n=17), other spring crops (n=18), set-aside (n=11) and Option 1B (n=7). Fine-scale habitat data was collected in the 2000 breeding season only.

3.2.1.3 *Data analysis*

A problem with interpreting the vegetation data at the nest-site, is that not all nests were found at the same stage of the incubation period. To overcome this problem the baseline ground surface data was used to produce simple models of crop height and cover over time for each crop type, using the standard curve fitting procedure in GENSTAT. Linear, logistic, generalised logistic and Gompertz curves were fitted to the data. For each crop type the curve that resulted in the least amount of residual variation was chosen as the best fitting model. From the resulting crop specific growth models it was possible to back calculate an expected crop height and cover at the time of nest initiation, i.e. first egg date, using the following procedure:

(Step 1)

$$\frac{\text{Growth model prediction of crop characteristic for day nest measures taken}}{\text{Model prediction of crop characteristic for first egg date}} \times 100 = \%\ \text{change}$$

(Step 2)

$$\frac{\text{Actual nest-site measurements}}{\%\ \text{change}} \times 100 = \text{calculated crop characteristic at nest-site for first egg date}$$

An arbitrarily determined r^2 value of greater than 0.7 was used to select if the models were of sufficient predictive power to be used in the back calculation procedure. Crop growth models (height and cover) were produced for all crop types (r^2 values for the models ranged from (0.7-0.95), with the exception of set-aside for which the growth models were a poor description of the data (r^2<0.2). For Option 1B the crop cover model was poor (r^2=0.24) and only the crop height model was used to back calculate measurements at the time of nest initiation. Vegetation growth was much slower in the non crop habitats of set-side and Option 1B compared to cropped habitats, and hence where the growth models were poor, unadjusted measures were used as vegetation is unlikely to have changed significantly in the time period between nest site initiation and nest location. These unadjusted and back calculated measurements were then used in the analysis of differences in crop characteristics between the nest-site, sites adjacent to the nest and random sites within the same field using analysis of variance or the equivalent non-parametric Kruskal Wallis test. Shapiro Wilks and Bartlett's tests were applied to the data sets to test for normality and homoscedasticity, respectively. Where multiple testing was used, a Dunn-Sidak correction was applied to obtain an experimentwise error rate (Sokal & Rohlf, 1995). For comparison of ground topography, nest-site and adjacent measurements (3 quadrats in total) were combined and compared to the random measures.

Logistic regression was undertaken using GLIM 3.77 to determine which of the vegetation characteristics were having significant effects on nest placement within fields. The response variable was the presence or absence of a nest, all models assumed a binomial error distribution and a logit link function was specified following Crawley (1993). The variables were highly correlated and so a step-up modelling procedure was adopted to identify which variables were having significant effects on nest placement in isoloation. Multivariate models using all combinations of the variables significant in univariate models were then fitted. The reduction in

residual deviance when entering each explanatory variable was treated as a likelihood ratio test and its significance assessed by comparing it with the chi-square distribution with the appropriate degrees of freedom.

3.2.2 Field-scale landscape data

The specific aim of this section is to identify key habitat and landscape characteristics associated with nest placement at the field-scale

3.2.2.1 *Nest-site characteristics*

A number of nest-site variables were required for this section of the study, which would necessitate unacceptable levels of disturbance to nesting Lapwings, possibly increasing the likelihood of desertion or increasing the risk of predation. Hence, at the end of all nesting attempts within that field, nests were relocated and the following variables were recorded: distance to the nearest neighbour, distance to the nearest field boundary, distance to the nearest predator perch (any vertical component >2m, usually a tree or telegraph pole), and distances to the nearest wood plot and pasture (in areas of low density of these two habitats the distance was often extracted from 1:10000 farm maps or 1:25000 Ordnance Survey maps). An arbitrarily determined maximum distance for all the above variables was 500m as it was felt that beyond that distance characteristics are highly unlikely to be strong determinants of Lapwing nest-site placement. Distances were measured by a fieldworker pacing between the two points and recording the number of paces, which were then converted to metres. The conversion was based on the fieldworker pacing out 10 paces and recording the distance in metres using a tape measure, this was repeated 10 times, and the average was taken as the conversion rate.

A field boundary index was recorded during the course of the breeding season using the method of Milsom *et al.* (2000) and Milsom *et al.* (1985). Each field boundary was assigned a score using the following scale of openness: 1, no fence or wall; 2, open fence; 3, discontinuous boundary (hedge, solid fence or wall); 4, continuous hedge, solid fence or wall <2m high; 5, hedge, solid fence or wall with widely spaced trees; 6, tree belt, hedge, solid fence or wall >2m high. If a boundary was

heterogenous in respect to the scores, a 'by eye' assessment was made of the proportions of each score. The boundary index was then calculated using the following equation:

$$\text{boundary}=(p_1 \times 1) + (p_2 \times 2) + (p_3 \times 3) + (p_4 \times 4) + (p_5 \times 5) + (p_6 \times 6)$$

where p_n is the proportion of the boundary of a field with a boundary score of n. Thus, the index varies from 1, completely open, to 6, completely enclosed by a boundary greater than 2m high.
The number of active pairs in each field was recorded by dividing the number of adults observed by two; personal observations suggest that monogamy is the dominant mating system in this population.

3.2.2.2 *Field characteristics*

For each field where a nest was located the following variables were recorded, crop type, field area (hectares) and boundary index. The area of nesting fields were determined either from asking farmers, or from 1:25000 OS maps. At the end of the breeding season the total number of nesting attempts for each field was established. A comparative field adjacent to each breeding field was selected randomly using the role of a dice, the only criteria being that the comparison field should not have been used for breeding by Lapwings in that particular field season. Data for this part of the study was collected over the two field seasons of 1999 and 2000.

3.2.2.3 *Data analysis*

Nest-site characteristics were analysed to investigate differences between crop categories. Shapiro Wilks and Bartlett's tests were applied to the data set to check for normality and homoscedasticity, respectively, and where appropriate data transformation was attempted to allow for the requirements of ANOVA. Failure to meet these requirements led to the adoption of the non-parametric equivalent Kruskal Wallis test. *Post hoc* testing using Tukeys HSD (ANOVA) and paired Mann Whitney tests (Kruskal Wallis) were carried out to determine those groups which

differed. Where multiple testing was used, a Dunn Sidak correction was applied (Sokal & Rohlf, 1995). Relationships between the variables were investigated using Spearman's *r* rank correlation.

A modelling approach was adopted in the analysis of the field characteristics data. The actual number of nesting attempts within a field during each breeding season (including comparative fields with zero counts) followed a Poisson distribution. GLIM 3.7 was used to model the data, declaring the number of nesting attempts as the response variable and assuming a Poisson distribution with a log-link function (Crawley, 1993). The variables to be included in the analysis were crop category (a 7-level factor of, winter crops, Option 1B, spring cereals, other spring crops, set-aside, all grass types, and all stubbles), field area and boundary index. As there may be a degree of spatial autocorrelation between fields that would increase the likelihood of Type I errors a dummy variable 'farm' (an 11-level factor, representing farm groupings) was forced into final MAMs.

Maximal models were fitted to the whole season data set and also to two further data sets incorporating all those nests that were determined as first nests and all those that were renesting attempts, to identify any temporal variation in factors that affect nest-site selection. By plotting pair formation periods, first egg dates and incubation periods, onto a time-series, estimates can be made of the date of the first possible re-nesting attempt. All nests started before this cut-off date were assumed to be first nesting attempts, and all nests after this date were assumed to be re-nesting attempts. An initial three stage modelling process dividing the data into months (March, April and May) was abandoned due to small data sets, particularly for May. Quadratic terms for field area and boundary index were calculated and entered into maximal models as were interaction terms. Each variable was deleted and returned sequentially to the model, the variable that explained the smallest reduction in deviance, as assessed by comparison to χ^2 at the appropriate degrees of freedom was deleted from the model. This process was repeated until only those variables which were significant were retained in Minimum Adequate Models. In all cases, overdispersion of the data was assumed if the ratio of the residual degrees of freedom exceeded 2.0. Where this was so, models were rescaled to a value of Pearson's χ^2 divided by the number of degrees of freedom (Aitkin *et al.*, 1989).

This type of linear modelling prohibits the calculation of meaningful r^2 values, as the variance is proportional to the mean in the resulting models. The fit of the models were assessed visually by plotting observed values against predicted values. To understand further the predictive power of these models, a logistic regression analysis was conducted, using a binomial error structure and a logit link function (Crawley, 1993) to model Lapwing presence or absence using the same explanatory variables above. The fitted probabilities of occurrence were then interpreted as predicted presence, predicted absence or prediction uncertain, using a series of thresholds that allocated an increasing proportion of intermediate values to the prediction uncertain category (Manel *et al.*, 1999; Bradbury *et al.*, 2000). A two-way classification table of observed presence and absence vs. predicted presence and absence was then constructed (Table 3.1) (Fielding & Bell, 1997).

Table 3.1. Basic two-way classification table used as a basis for testing model performance of presence-absence models. The table cross-tabulates actual presence/absence (derived from model fitted values) against those predicted. *a*=true positive values; *b*=false positives; *c*=false negatives; *d*=true negatives (after Fielding & Bell, 1997; Manel *et al.*, 2001).

		Observed	
		+	-
Predicted	+	*a*	*b*
	-	*c*	*d*

The overall prediction success of the logistic models were evaluated by calculating the percentage of all cases that were correctly predicted. Using Table 3.1 this is derived from:

$$a+d/n$$

Where n is the number of cases. However, a model may be 'good,' but the habitat may not be saturated, because of low population size or a limiting factor in another stage of the life cycle, therefore absence may be predicted better than presence. Separate assessments of predictive

power for absence and presence were undertaken. Furthermore, although the percentage of cases correctly predicted is widely used as a measure of evaluating model performance, Manel *et al.* (2001) show that in some instances this can be misleading. An alternative is to use Cohen's kappa, a measure of the proportion of all possible cases of presence or absence that are predicted correctly after accounting for chance effects (Fielding & Bell, 1997). Using Table 3.1, Cohen's kappa is calculated by:

$$\frac{[(a+d)-(((a+c)(a+b)+(b+d)(c+d))/n)]}{[n-(((a+c)(a+b)+(b+d)(c+d))/n)]}$$

Where n is the number of cases. Values 0-0.4 are considered to indicate slight to fair model performance, values of 0.4-0.6 moderate, 0.6-0.8 substantial and 0.8-1.0 almost perfect (Landis & Koch, 1977). Although this categorization of model performance is an arbitrary assessment, values of kappa offer a meaningful numerical variable for comparison of models (Manel *et al.*, 2001).

3.2.3 1km^2 landscape data.

The specific aim of this section is to identify large-scale cropping patterns that influence nest placement.

3.2.3.1 *Data collection.*

Once the nesting period was completed (end of June), fields that had nesting pairs were plotted onto Ordnance Survey maps (1:25,000 Landranger Series). 1km^2 grid squares where Lapwings were known to be present were surveyed to ascertain the crop type within each field. Field area (in hectares) was measured from farm maps or 1:25,000 OS maps. A (randomly determined) corresponding 1km^2 where breeding Lapwings were not recorded was also surveyed. The proportion of each crop type in each square was estimated. One disadvantage of leaving the data collection till the end of the breeding season was that the availability of stubble fields at nest

initiation were not recorded as all fields had of course been cultivated and planted. This was however unavoidable due to constraints of time and manpower. Data for this part of the study was collected in the 2000 field season only.

3.2.3.2 *Data analysis.*

Nest placement at the $1km^2$ scale was analysed using two separate modelling procedures in GLIM 3.77. Firstly, the number of nesting attempts was selected as the response variable, and the proportions of each crop type in each grid square were treated as explanatory variables. The data followed a Poisson distribution, and a log link function was specified (Crawley, 1993). A number of the variables were highly correlated and so a step-up modelling procedure was adopted to identify which variables were having significant effects on nest placement. Multivariate models using all combinations of the variables significant in univariate models were then fitted. The data set was divided into first attempts and replacement nests (as section 3.2.2.3) and the same procedure was undertaken to identify temporal changes in cropping patterns that may influence Lapwing nest placement.

Using the same data set, logistic regression models evaluating the presence or absence of nesting Lapwings in a $1km^2$ was undertaken. The response variable was binomial and logit link function was specified (Crawley, 1993). Again, separate data sets were used for first and replacement clutches to investigate temporal changes in cropping patterns and any possible influence on the presence or absence of nesting Lapwings. Interpretation and assessment of performance of logistic models was the same as outlined in section 3.2.2.3.

3.3 RESULTS

3.3.1 Fine-scale habitat selection at the nest-site

3.3.1.1 *Crop height*

Crop height at the nest-site was strongly influenced by crop type. There were differences in mean crop height between crops, with winter cereal being on average 72mm tall (range=32-125mm) and spring crops the lowest mean height at 8mm (range=0-55mm). These between crop differences were significantly different between certain crop categories (Kruskal Wallis H=52.46, 6 d.f., P= <0.001). *Post hoc* testing using Mann Whitney paired tests identify which crop categories were different from each other (Table 3.2).

In winter cereals there was a significant difference in crop height between within field measurements (F=$5.99_{2, 42,}$ P= <0.005). *Post hoc* testing (Tukey's HSD test) shows that height of the crop at nest-sites did not differ from the area adjacent to the nest-site (P=0.96) but crop height at both the nest-site and adjacent to it was significantly shorter in comparison to random measurements (P= <0.05) (Table 3.3). The only other crop that differed in crop height between different within field measurements was the Option 1B category (Kruskal Wallis H=11.01, 2 d.f., P=<0.05) where average crop height at the nest was shorter than random measurements (Mann Whitney U=14.5, P=<0.001) (Table 3.4).

3.3.1.2 *Crop cover*

Differences in percentage crop cover at the nest-site between crop categories were significant (Kruskal Wallis H=51.94, 6 d.f., P=<0.001). *Post hoc* testing using Mann Whitney tests shows that nests in winter cereals were in areas of more crop cover than all other crop types (Table 3.5).

Within crop types there were no significant differences in crop cover between different within field measurements. Winter cereal nests were in areas of less crop cover than would be expected at random (Kruskal Wallis H=6.007, 2 d.f., P=<0.05), but once adjustments were made for multiple testing, the result was non-significant.

Table 3.2. Results of Mann Whitney paired tests identifying crop categories which differ in relation to average crop height at the nest-site at the time of nest initiation, **P*<0.05, ***P*<0.01, ****P*<0.001. Adjustments for multiple testing have been applied (see text). The mean (and standard error) and maximum height (mm), at the nest-site at nest initiation are given for each crop for comparison.

	Mean height (mm)	Max. height (mm)	Winter cereal	Winter beans	Spring crops	Stubble	Option 1B	Spring cereal
Winter cereal	72 ±7.1	125						
Winter beans	55 ±12.6	112	n.s.					
Other spring crops	8 ±3.6	55	***	**				
Stubble	36 ±3.9	61	**	n.s.	**			
Option 1B	10 ±4.2	44	***	*	n.s.	*		
Spring cereals	33 ±6.2	109	**	n.s.	**	n.s.	*	
Set-aside	48 ±5.9	116	n.s.	n.s.	**	n.s.	*	n.s.

Table 3.3. Results of ANOVA on crop height (mm) between different within field measurements (see text for details) within crop categories. *Post hoc* testing using Tukey's HSD test identifies those measurements for which the differences are significant, means with the same superscript number within rows are different, [1,2] $P<0.05$. Note, spring cereal data were log transformed prior to ANOVA to normalise the distribution, however, the figures presented here are back transformed to aid comparison with other crop categories.

Crop category	*F*	*P*-level	Nest	Adjacent	Random
Winter cereal	5.99	0.005	72^{1}	75^{2}	$106^{1,2}$
Winter beans	0.28	0.76	55	56	66
Set-aside	0.72	0.49	43	51	55
Spring cereal	0.12	0.89	33	35	39

Table 3.4. Median values for crop height (mm) between different within field measurements (Kruskal Wallis analysis). Mann Whitney tests were performed on each pair of groups to identify those measurements at which the differences are significant, medians with the superscript[1] were significantly different from each other, $P<0.005$. Mean values are also given in parentheses to aid comparison with Table 3.3.

Crop category	H	*P*-level	nest	adjacent	random
Other spring crops	0.08	0.96	0.0 (8)	0.0 (8)	0.0 (7)
Option 1B	11.01	0.004	$0.0\ (10)^{1}$	2.1 (22)	$3.6\ (34)^{1}$

Table 3.5. Results of Mann Whitney paired tests identifying which crop categories are different from each other in relation to average crop cover (%) at the nest-site at the time of nest initiation, **P*<0.05, ***P*<0.01, ****P*<0.001. The mean (and standard error) and maximum percentage crop cover at the nest at nest initiation are given for each crop for comparison.

	Mean cover (%)	Max. cover (%)	Winter cereal	Winter beans	Spring crops	Stubble	Option 1B	Spring cereal
Winter cereal	48 ±6.98	86						
Winter beans	5 ±1.4	10	**					
Other spring crops	1 ±0.54	7	***	*				
Stubble	14 ±5.83	69	**	n.s.	**			
Option 1B	5 ±2.51	29	***	n.s.	n.s.	n.s.		
Spring cereals	14 ±3.34	61	**	n.s.	***	n.s.	n.s.	
Set-aside	3 ±2.21	16	**	n.s.	n.s.	n.s.	n.s.	n.s.

3.3.1.3 *Ground topography*

Sample sizes for nests on winter beans and stubbles were too small for analysis. There were differences in ground topography variability between crop types (Kruskal Wallis H=22.83, 4 d.f., P=<0.001) (Figure 3.1), and nests in non-cropped fields (ie set-aside and Option 1B) had a greater degree of variability in comparison to each of the other crop types (Table 3.6). However, following corrections for multiple testing the difference between ground topography on set-aside and winter cereals was no longer significant. There were no differences in ground topography between the nest-site and random measurements in any of the crop categories.

3.3.1.4 *Vegetation diversity.*

There were differences in vegetation diversity scores between crop types (Kruskal Wallis H=44.9, 5 d.f., P=<0.001) (Figure 3.2, Table 3.7) and nests in non cropped fields were associated with more diverse vegetation composition than those nests in cropped habitats. There were no differences in vegetation diversity scores between the nest site and random measurements in any of the crop categories.

Table 3.6. Results of Mann Whitney paired tests identifying which crop categories are different from each other in relation to ground topography index at the nest-site at the time of nest initiation, *P<0.05, **P<0.01, ***P<0.001. Adjustments for multiple testing have been applied (see text).

	Winter cereal	Spring crops	Option 1B	Spring cereal
Winter cereal				
Other spring crops	n.s.			
Option 1B	**	***		
Spring cereals	n.s.	n.s.	***	
Set-aside	n.s.	*	n.s.	**

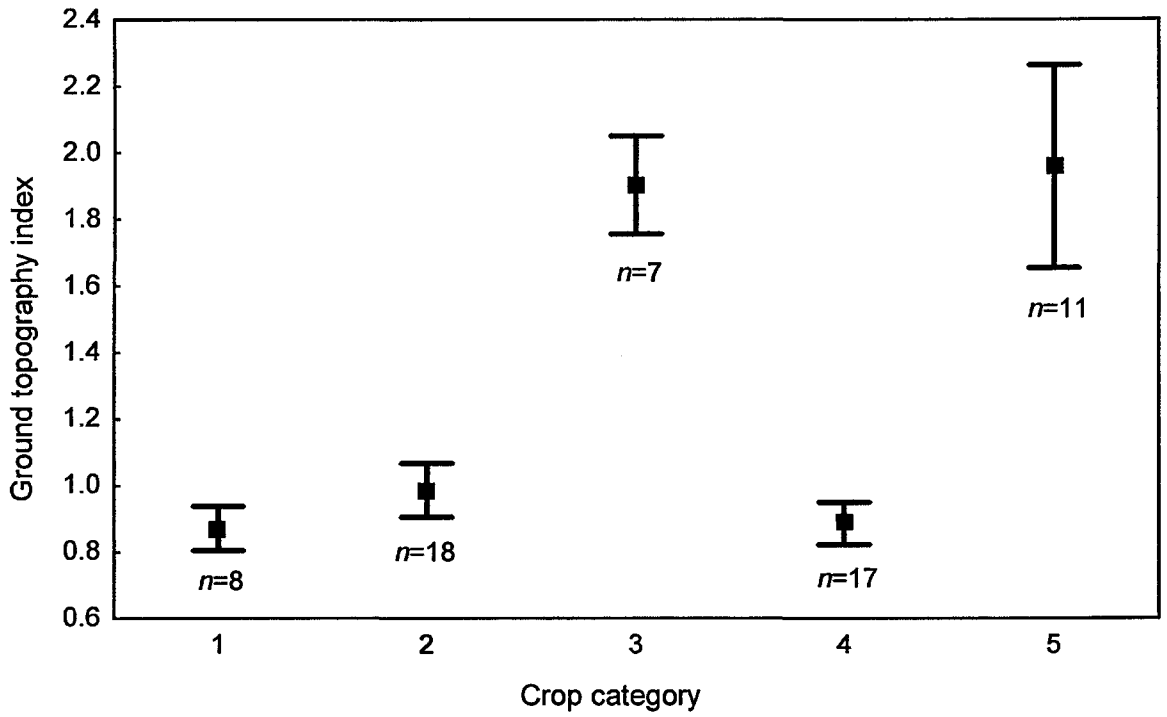

Figure 3.1. The mean ground topography index (see text for details) at the nest-site at nest initiation by crop category, where 1=winter cereals, 2=spring crops (excluding cereal), 3=Option 1B, 4=spring cereal, 5=set-aside. There was as a significant difference between categories (Kruskal Wallis H=22.83, 4 d.f., $P<0.001$). Means with one standard error are shown.

Table 3.7. Results of Mann Whitney paired tests identifying which crop categories are different from each other in relation to vegetation diversity scores at the nest-site at the time of nest initiation, $*P<0.005$, $**P<0.001$. (Adjustments for multiple testing have been applied).

	Winter cereal	Winter beans	Spring cereal	Spring crops	Option 1B
Winter cereal					
Winter beans	n.s.				
Spring cereal	n.s.	n.s.			
Spring crops	**	n.s.	*		
Option 1B	n.s.	n.s.	n.s.	**	
Set-aside	*	*	**	**	n.s.

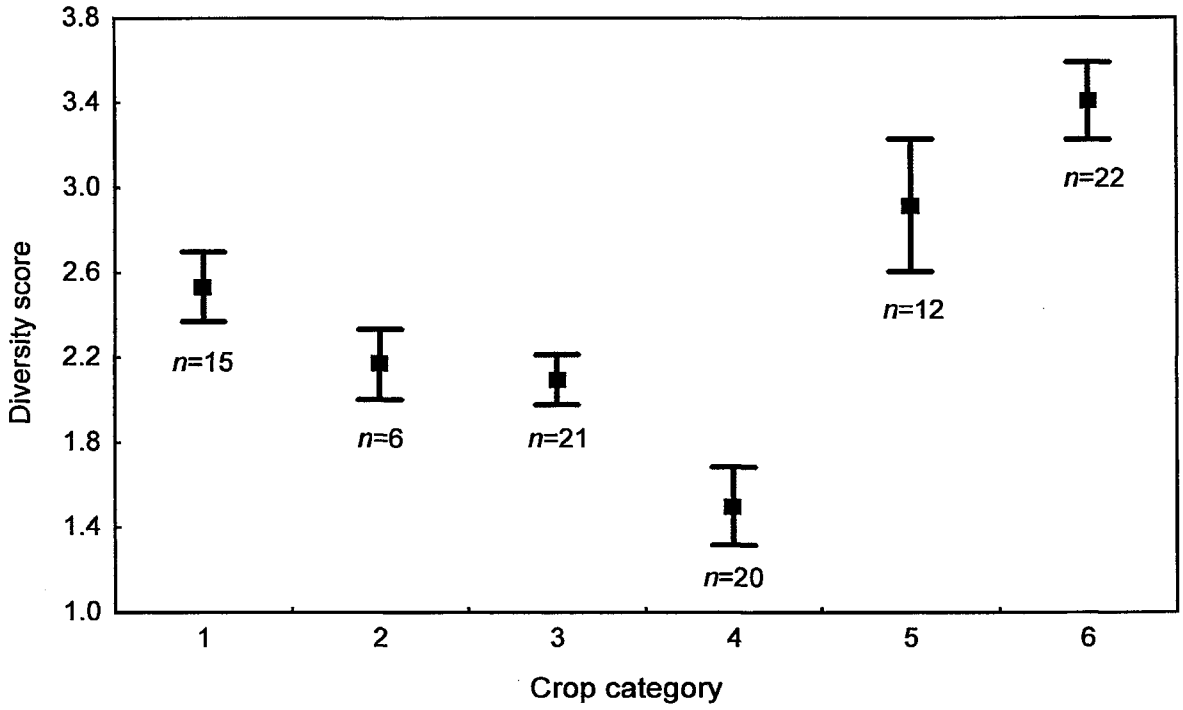

Figure 3.2. Mean vegetation diversity scores at the nest-site at nest initiation by crop category, where 1=winter cereal, 2=winter beans, 3=spring cereal, 4=spring crops, 5=Option 1B, 6=set-aside. There was a significant difference between categories (Kruskal Wallis H=44.89, 5 d.f., $P<0.001$). Means with one standard error are shown

3.3.1.5 *Logistic regression*

There were no significant differences between any of the measured variables at the nest-site and the area adjacent to the nest, as outlined above, so the two sets of measurements were combined, and then compared with the random measurements using logistic regression. Crop height, crop cover and bare ground were shown to be significantly different in the area surrounding the nest in winter cereals. The only other detectable effect was that of crop height on nest placement within Option 1B (Table 3.8). Crop height, crop cover and bare ground were highly correlated and none of the variables could be combined to give a significant multivariate model. Crop height accounts for the largest reduction in residual deviance (Table 3.8), suggesting that crop height is the most important sward characteristic in determining Lapwing nest placement within fields.

Table 3.8. Summary of vegetation characteristics by crop type, comparing characteristics at and adjacent to the nest-site and at random within the same field (see text for details). Univariate models were fitted to examine the effects of each variable (significant χ^2 are given), $*P<0.05$, $**P<0.01$. The sign of the parameter estimate is given in parentheses.

	Crop height	Crop cover	Bare ground	Diversity index
Winter cereal	χ^2=7.532**(-)	χ^2=6.106*(-)	χ^2=6.527*(+)	n.s.
Spring cereal	n.s.	n.s.	n.s.	n.s.
Other spring crops	n.s.	n.s.	n.s.	n.s.
Option 1B	χ^2=8.089**(-)	n.s.	n.s.	n.s.
Set-aside & stubbles	n.s.	n.s.	n.s.	n.s.

3.3.2 Field-scale landscape data.

A total of 188 nests were located on a broad range of crop types (Figure 3.3). The first possible re-nesting attempt in 1999 was initiated on the 28th April, and in 2000 on the 24th April. All nests initiated prior to these dates were considered first clutches, and after these dates were presumed to be replacement clutches. First clutches (n=136) tended to be on a wide range of both cropped and non-cropped habitats (Figure 3.4) with a reduced range of crops chosen for replacement clutches (n=52) (Figure 3.5). To maintain adequate sample sizes for statistical analyses the following crop classifications were used; winter crops (n=27), spring cereal (n=28), other spring crops (n=37), set-aside (n=27), Option 1B (n=34), grass (n=17), and stubbles (n=18). There were differences between crop types in relation to a number of the measured field-scale variables (Table 3.9).

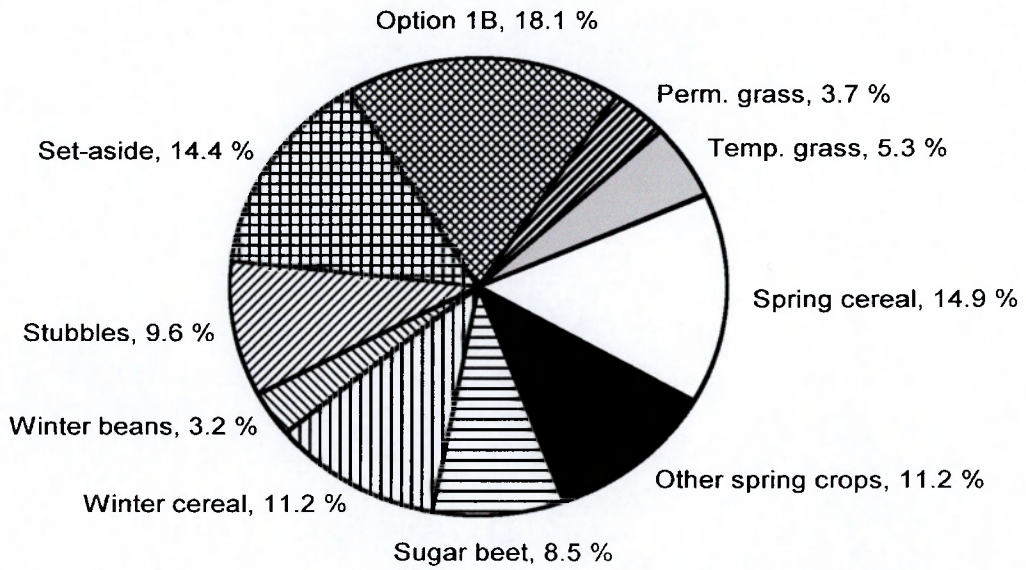

Figure 3.3. Distribution of Lapwing nests in relation to crop type. Data presented from all 188 nests over the whole breeding season.

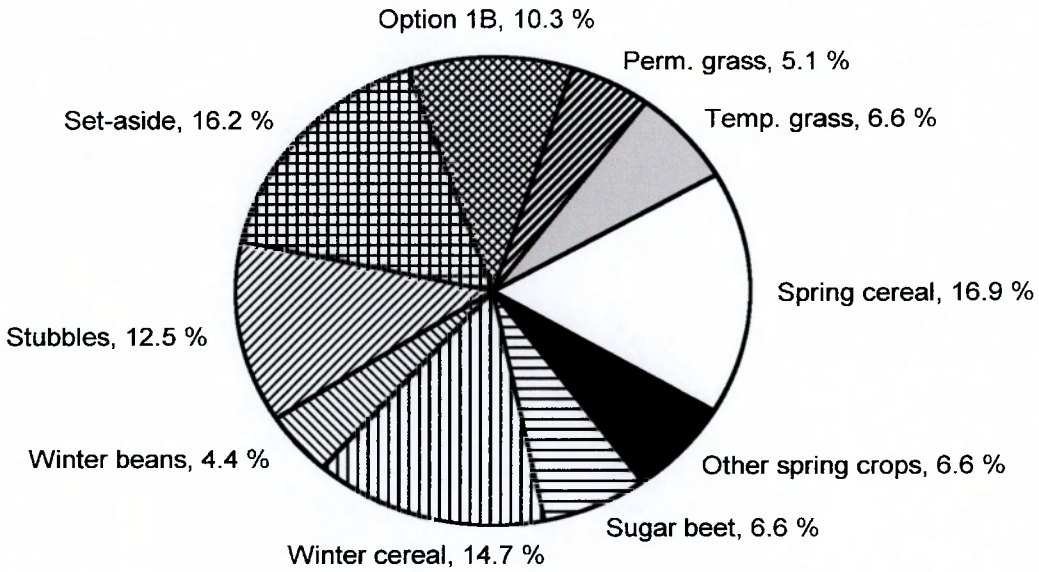

Figure 3.4. Distribution of Lapwing nests in relation to crop type. Data presented from all 136 nests which were first clutches (see text for definition).

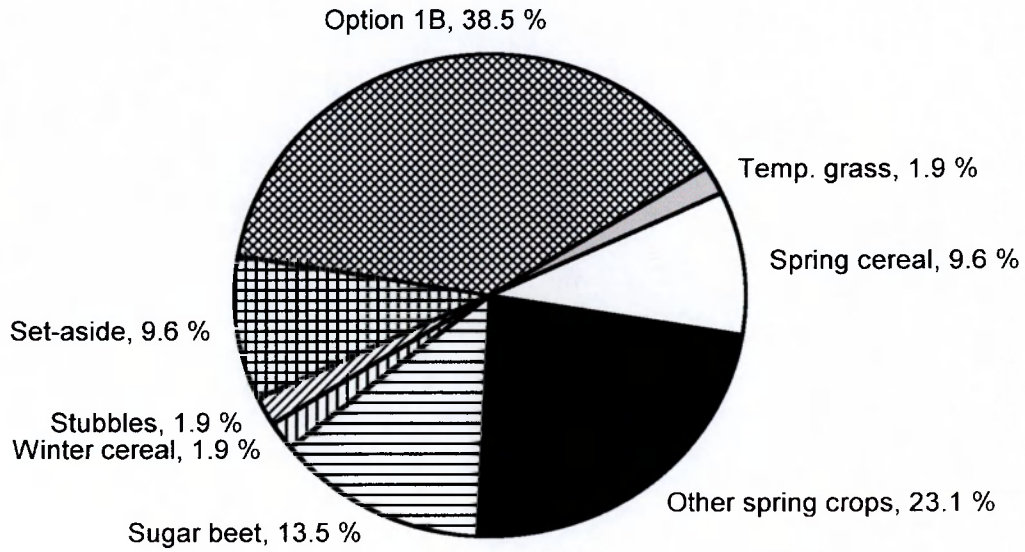

Figure 3.5. Distribution of Lapwing nests in relation to crop type. Data presented from all 52 nests which were replacement clutches (see text for definition).

3.3.2.1 *Number of active pairs*

Only 12% of breeding attempts had no other neighbouring nest within the same field (Figure 3.6). Nests on Option 1B fields tended to be associated with the most number of active pairs (5.4±0.3, range 2-7) with spring cereals having the lowest number (2.7±0.4, range 1-6). The average field area between crop types differed (Table 3.9), although the correlation with number of pairs is weak (Table 3.10) a better way of expressing the number of pairs is density of breeding pairs per field (Figure 3.7).

3.3.2.2 *Distance to predator perch*

Spring cereal nests were furthest away from predator perches (115.8m±10.2m, range 40m-280m) and nests on set-aside the closest (53.0m±3.9m, range 21m-107m). Much of these differences may be explained by inherent differences between crops in relation to field size, although nests on winter crops were significantly closer to predator perches than were nests on spring cereals, P=0.014 (Tukey test) (Table 3.9) despite having similar field area.

3.3.2.3 *Distance to field boundary*

Distance to the nearest field boundary was highly correlated with distance to the nearest predator perch (r=0.72, P=<0.001), and with field area (r=0.54, P=<0.001) (Table 3.10). Nests in small fields (set-aside, grass and Option 1B) tended to be closer field boundaries than larger fields (winter crops, spring cereal and other spring crops) (Table 3.9). There is no difference between distance to field boundary between winter crops and spring cereals (P=0.99) (Table 3.9).

3.3.2.4 *Distance to pasture and wood plots*

All the nests that were on grass fields were excluded from the ANOVA and the analysis was undertaken on 6 crop categories, there was no significant difference between crop categories in relation the distance between the nest and the nearest pasture field (Table 3.9). Nests on set-aside were closer to wood plots than on all other crop types (average 179.8m±22.8m, range 56m to

500m). There was a weak but significant correlation between distance to wood plot and distance to predator perch (Spearman's $r = 0.17$, $P=0.02$) (Table 3.10).

3.3.2.5 *Distance to nearest neighbour*

There are correlations between the distance to the nearest neighbour and both the number of active pairs (Spearman's $r=-0.70$, $P=<0.001$) and field area (Spearman's $r=0.37$, $P=<0.001$) across all crop categories (Table 3.10). Nests on grass and Option 1B tend to be in closer proximity to neighbours both with an average of 34m, those nest on spring cereals and other spring crops tend to have the greatest distance between nearest neighbours.

3.3.2.6 *Field area and boundary index*

There were significant differences between crop categories in relation to their associated field size (Kruskal Wallis, H=71.09, 6 d.f., $P=<0.001$). Spring cereals, winter crops, other spring crops and stubbles had the largest field area and were significantly larger than grass fields and the non-cropped habitats of Option 1B and set-aside (Table 3.9). Field area was correlated with distance to predator perch, distance to field boundary and distance to the nearest neighbour (Table 3.10).

The overall boundary index associated with nesting fields was 4.3 (Table 3.9), suggesting that nesting fields were characterised by boundaries with a vertical component of less than 2m. Boundary indices between crop categories were significantly different (Kruskal Wallis, H=27.05, 6 d.f., $P=<0.0001$), although the differences were small. Winter crops and set-aside fields tended to have the greater boundary indices, and Option 1B the smallest index (Table 3.9). All correlations between boundary index and other variables were weak (Table 3.10).

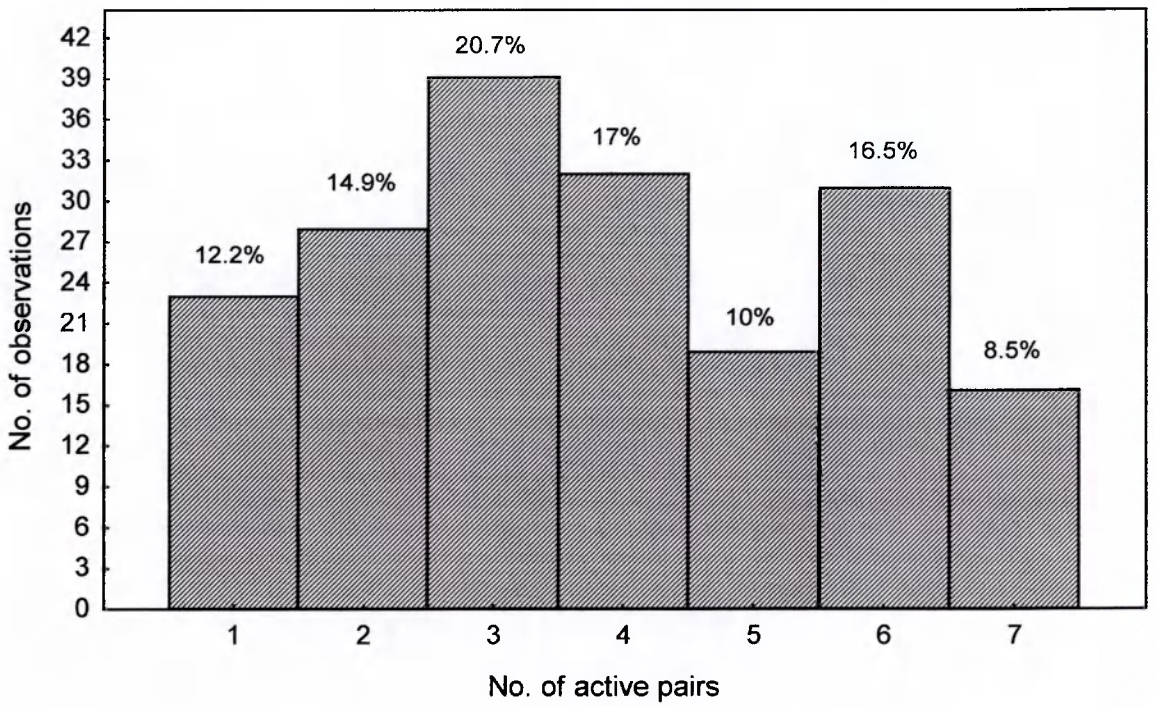

Figure 3.6. Colony size of Lapwings breeding on fields during 1999 and 2000 irrespective of crop category (188 nests). A detailed breakdown of inter-crop differences is given in Table 3.9.

Table 3.9. Summary of field-scale nest-site characteristics by crop type. See notes below to assist interpretation of data. The relevant F ratios and H scores are given, and categories significantly different from each other (as identified by Tukey's or Mann Whitney tests) are identified by subscripts of the same letter. *P<0.01, **P<0.001.

	N	A.P.†	D.P.P.§	D.F.B.‡	D.Pas.§‡	D.Wood	D.N.N.	Field area	M.B.I.
F ratio (ANOVA)		9.22**	10.38**	6.53**	n.s.				
H scores (Kruskal Wallis)						35.96*	33.80**	71.09**	27.05**
All nests	188	3.8±0.1	79.6±3.3	68.9±2.5	248.2±11.6	289.3±9.3	79.7±8.3	7.1±0.3	4.3±0.05
Winter crops	27	3.6±0.3^{a}	82.2±10.8^{a}	76.6±6.3^{ab}	338.4±30.0	283.6±25.7^{a}	70.6±10.9^{abc}	9.8±1.1^{abc}	4.6±0.08^{ab}
Spring cereal	28	2.7±0.4^{bc}	115.8±10.2^{abcd}	81.4±7.0^{cd}	250.4±32.1	313.8±28.5^{c}	108.9±21^{def}	10.4±0.7^{def}	4.3±0.08^{acd}
Other spring crops	37	3.0±0.2^{de}	95.8±6.3^{efg}	85.4±6.5^{ef}	225.5±21.3	337.6±15.1^{bd}	118.7±25.3^{gh}	8.7±0.8^{ghi}	4.1±0.14^{e}
Set-aside	27	3.9±0.4^{f}	53.0±3.9^{beh}	50.7±3.7^{ace}	272.3±32.0	179.8±22.8^{abcefg}	96.1±27.5	4.8±0.4^{adg}	4.6±0.14^{cef}
Option 1B	34	5.4±0.3^{abdf}	57.2±3.7^{cf}	51.5±4.0^{bdf}	241.0±24.1	259.2±13.1^{de}	34±3.4^{adh}	3.9±0.3^{behj}	3.9±0.1^{bdf}
Grass	17	3.5±0.2	55.4±5.6^{dg}	53.0±5.2	83.76±12.9	302.5±24.4^{f}	34.1±2.7^{be}	4.1±1.4^{cfik}	4.5±0.25
Stubbles	18	4.9±0.5^{ce}	91.2±10.3^{h}	78.8±9.3	288.4±41.0	369.4±35.6^{g}	72.8±35.6^{cfg}	7.3±0.7^{jk}	4.2±0.2

† data square root transformed for analysis, and back transformed for ease of comparison
§ data $\log^{10+1}$ transformed for analysis, and back transformed for ease of comparison
‡ analysis of distance to pasture data, excludes the category 'grass' from the analysis, as many of these were on pasture fields.
A.P. the number of active breeding pairs within the same field
D.P.P. the distance from the nest to the nearest predator perch
D.F.B. the distance from the nest to the nearest field boundary
D.Pas. the distance from the nest to the edge of the nearest pasture field
D. Wood the distance from the nest to the edge of the nearest wood plot
D.N.N. the distance from the nest to the nearest incubating neighbour
M.B.I. boundary index (1-6), see text for details

Table 3.10. Correlation matrix showing the relationship between all field-scale nest-site variables. All correlations are Spearman's *r*. See Table 3.9 for heading abbreviations.

Variable	D.N.N.	A.P.	D.P.P.	D.F.B.	D.Wood	D.Pas.	M.B.I.
D.N.N.							
A.P.	-0.699						
D.P.P.	0.158	-0.056					
D.F.B.	0.046	0.03	0.715				
D.Wood	0.116	-0.177	0.170	0.141			
D.Pas.	-0.078	0.212	0.026	0.052	-0.199		
M.B.I.	0.046	-0.05	-0.089	-0.001	-0.176	-0.192	
Field area	0.367	-0.097	0.613	0.541	0.130	0.099	0.032

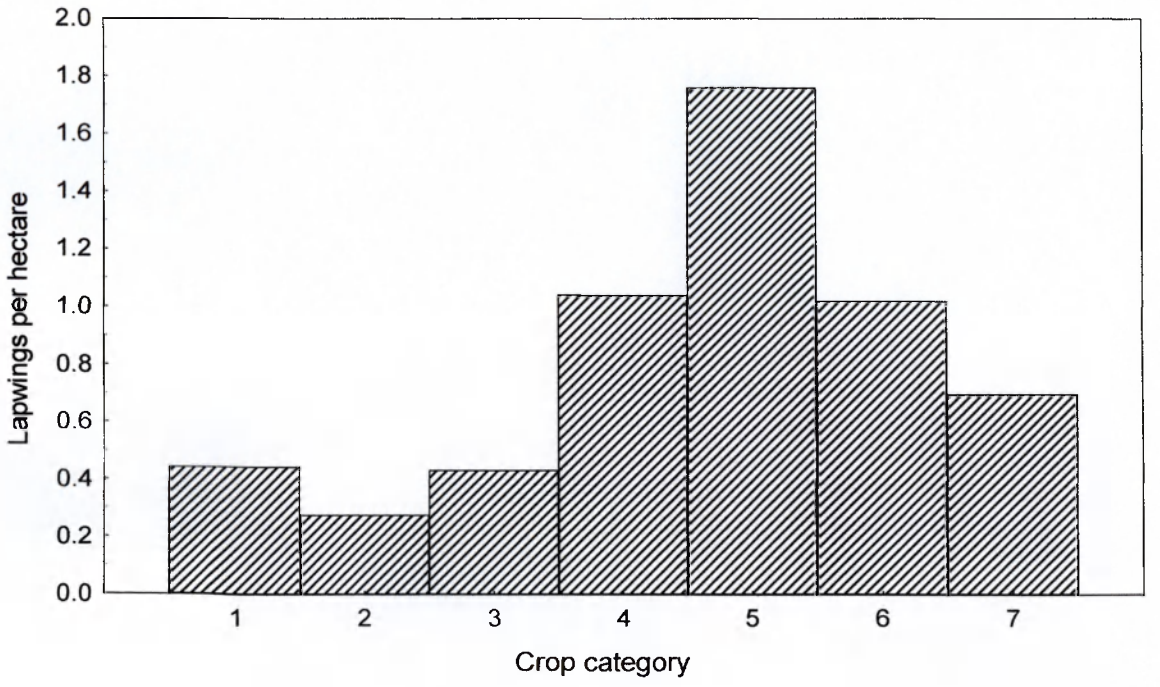

Figure 3.7. Breeding density of Lapwing pairs in nesting fields per hectare by crop type. Where, 1=winter crops, 2=spring cereal, 3=other spring crops, 4=set-aside, 5=Option 1B, 6=grass, and 7=stubbles.

3.3.2.7 Breeding attempts per field

In all time periods the crop categorical variable was retained in the final Poisson models, with field area being retained in the whole season and first nests models (Table 3.11a). Predictive power of the resulting models can be assessed visually by plotting model predicted values against observed values (Figures 3.8-3.10). It is evident that these results should be interpreted with consideration to the poor fit of the resulting models. No other variables approached significance, and no quadratic or interaction terms were retained in any MAMs. There was no evidence to suggest that there was any serious degree of spatial autocorrelation within the dataset as a farm term entered into all MAMs was non-significant.

Similarly, for logistic regression analyses crop type was retained in all MAMs, along with field area for the whole season and first nest models (Table 3.11b). All interaction and quadratic terms were deleted from the models and a farm term was non-significant when entered into final MAMs. Model performance of the logistic models are assessed in Table 3.12. Cohen's kappa values range from 0.42 to 0.73, suggesting that model performance was fair to substantial. The use of an increasingly stringent threshold tends to lead to improved model performance but sample sizes decrease (Table 3.12). For the whole season model the tendency was for absences to be predicted better than presence, but the converse was true for the first nests model.

Table 3.11. Minimal Adequate Models for a) the number of breeding attempts made per field (Poisson models), and b) presence or absence of breeding Lapwings in a field (logistic regression models). The change in residual deviance caused by removing each variable from the MAM is given with its significance value *P<0.05, **P<0.01, ***P<0.001. The sign of the parameter estimate is given in parentheses. The ratio of residual deviance to residual degrees of freedom is given to assist in model interpretation (Table a only). The dummy variable 'farm' is shown to highlight the lack of spatial autocorrelation within the dataset.

a) Poisson regression models

Variable	df	Whole season	First nests	Re-nests
Crop type	6	27.97***	19.06**	50.68***
Field area	1	7.62*(+)	3.98*(+)	n.s.
M.B.I.	1	n.s.	n.s.	n.s.
Farm	10	n.s.	n.s.	n.s.
Ratio		0.91	0.89	1.17

b) Logistic regression models

Variable	df	Whole season	First nests	Re-nests
Crop type	6	18.41**	17.29**	19.17**
Field area	1	4.68*(+)	5.18*(+)	n.s.
M.B.I.	1	n.s.	n.s.	n.s.
Farm	10	n.s.	n.s.	n.s.

Table 3.12. Two-way classification table (see Table 3.1) derived from significant bivariate logistic regression models predicting the presence or absence of Lapwings in an individual field. Fitted probability estimates varied from 0 to 1 and these were used to predict absence and presence using a series of increasingly stringent thresholds. To assist in model interpretation the percentage of all correctly predicted cases, the percentage of correctly predicted absences, the percentage of correctly predicted presences and Cohen's kappa are given.

		0-0.49:0.5-1.0		0-0.35:0.65-1.0		0-0.2-0.8-1.0	
		Observed (+)	Observed (-)	Observed (+)	Observed (-)	Observed (+)	Observed (-)
Whole season model	Predicted (+)	42	21	20	14	13	3
Crop category+field area	Predicted (-)	17	51	6	33	0	2
	% correct predictions	71%		71%		83.3%	
	% correct absences	75%		84.6%		100%	
	% correct presences	67.7%		58.9%		81.3%	
	Cohen's kappa	0.42		0.5		0.49	
First nests model	Predicted (+)	32	10	18	3	12	1
Crop category+field area	Predicted (-)	20	47	13	26	1	4
	% correct predictions	72.5%		73.3%		88.9%	
	% correct absences	70.1%		66.7%		80%	
	% correct presences	76.2%		85.7%		92.3%	
	Cohen's kappa	0.44		0.47		0.73	

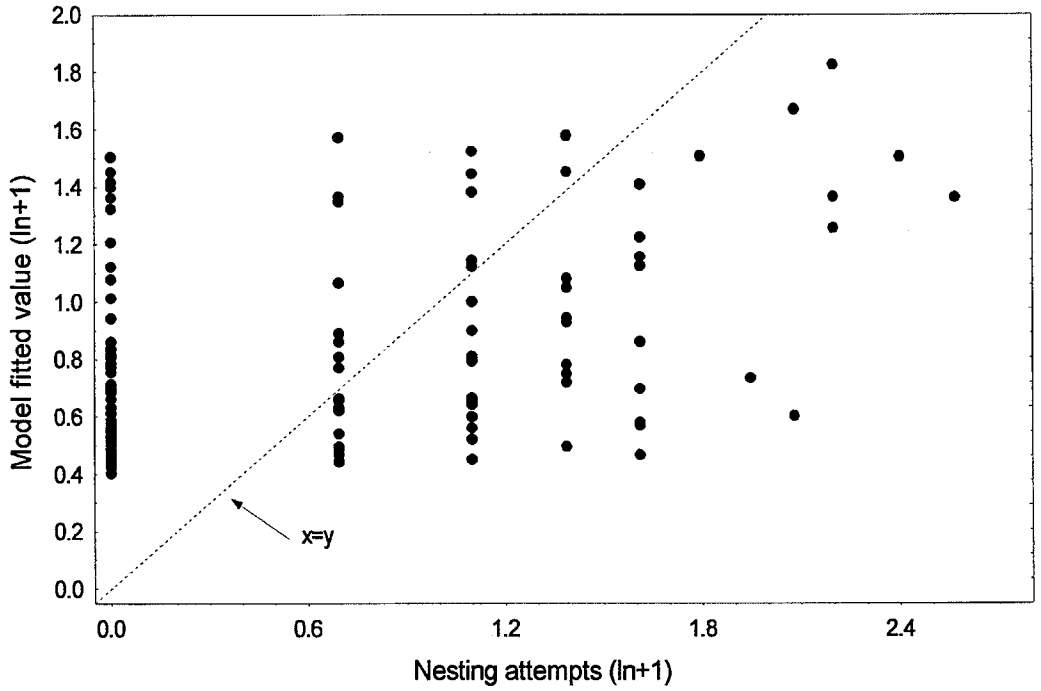

Figure 3.8. Scatterplot of log transformed model fitted value from the poisson models. The whole season data set. x=y (perfect relationship) is shown by the dotted line.

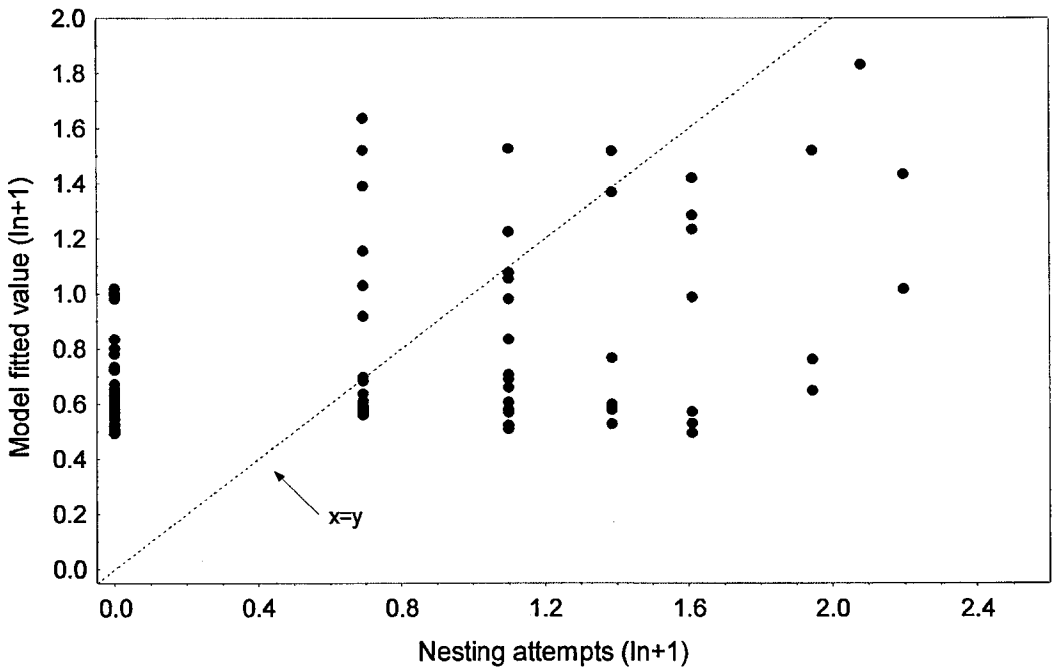

Figure 3.9. Scatterplot of log transformed model fitted value from the poisson models. The first nesting attempts data set. x=y (perfect relationship) is shown by the dotted line.

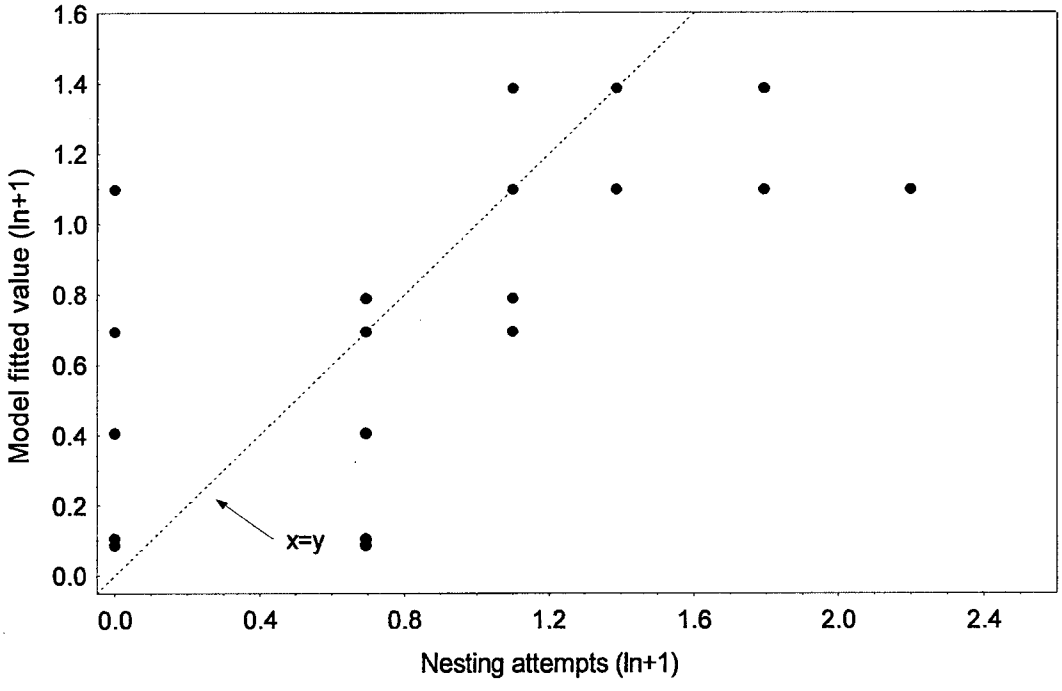

Figure 3.10. Scatterplot of log transformed model fitted value from the poisson models. The re-nesting attempts data set. x=y (perfect relationship) is shown by the dotted line.

3.3.3 1km^2 landscape data

Lapwings bred in a total of 24km grid squares which were surveyed to ascertain crop cover estimates along with a further 24 comparison squares. To maintain adequate sample sizes for analysis the number of crop categories were reduced to the following; winter cereals, all other winter crops, spring cereals, all other spring crops, Option 1B, all set-aside, all grass, and a miscellaneous category. A further 2 categories were used, all winter tillage (winter cereals + all other winter crops) and spring tillage (spring cereals + all other spring crops).

The overall number of Lapwing nesting attempts in a single grid square ranged from 1-13 (mean=5.29, s.d.=3.5), the number of first nests ranged from 0-12 (mean=3.96, s.d.=3.24), and the number of renests ranged from 0-3 (mean=1.33, s.d.=1.13).

Significant univariate models are given in Table 3.13. Winter cereals and winter tillage are highly correlated (Spearman's r=0.92, P=<0.001), with a negative correlation between winter cereals and spring cereals (Spearman's r=-0.46, P=<0.01), and winter tillage and spring cereals (Spearman's r=-0.51, P=<0.001).

Table 3.13. Significant univariate models derived from Poisson models. The change in residual deviance is given with its significance value, *<0.05, **<0.01. The sign of the parameter estimate is given in parentheses.

Variable	All nests	First nests	Renests
Winter cereal	6.718**(-)	3.906*(-)	4.967*(-)
Winter tillage	6.265*(-)	4.255*(-)	4.182*(-)
Spring cereal	n.s.	4.221*(+)	n.s.
Option 1B	n.s.	n.s.	4.456*(+)

Due to the highly correlated nature of the significant univariate models they could not be combined and entered into the same mutivariate models. The exception to this was with the renesting dataset where winter cereals and Option IB were both retained in a significant bivariate model (χ^2=9.15, d.f., 2). In all instances the area of winter cereals and winter tillage are shown to

have a negative effect on the number of birds that are present within a $1km^2$, and spring cereals and Option1B a positive effect (Table 3.13). An effect of the area of grass habitats in a $1km^2$ was not evident in any of the datasets but approached significance in the renesting data (χ^2=3.7, n.s. d.f.,1). Similar results were obtained from logistic regression models (Table 3.14). There was an apparent positive effect of the area of spring cereals in both the whole season dataset (χ^2=4.53) and the first nests (χ^2=6.86), and for the renesting dataset the area of grass had a positive influence (χ^2=6.61) on the presence or absence of breeding Lapwings in a given 1 km grid square (Table 3.14).

As in the Poisson models the correlated nature of some variables meant they could not be combined in multivariate models. However, for the renesting data, multivariate models containing winter cereal and Option 1B (χ^2=11.29) and Option 1B and grass (χ^2=10.25) were both significant. The models were generally better at predicting absence of breeding Lapwings in a grid square rather than presence, although the difference is slight (Table 3.15). The percentage of overall correctly predicted cases increases as the fitted probability estimates become increasingly stringent, although the sample size decreases to as low as 14 (Table 3.15). Cohen's kappa ranges from 0.35-0.6 suggesting that model performance is fair to moderate (Table 3.15).

Table 3.14. Significant univariate models derived from logistic regression used to predict the presence or absence of breeding Lapwings in a $1km^2$. The change in residual deviance is given with its significance value, *<0.05, **<0.01. The sign of the parameter estimate is given in parentheses.

Variable	All nests	First	Re-nests
Winter cereal	9.42**(-)	4.44*(-)	6.24*(-)
Winter tillage	8.09**(-)	5.03*(-)	4.94*(-)
Spring cereal	4.53*(+)	6.86**(+)	n.s.
Option 1B	n.s.	n.s.	6.08*(+)
Grass	n.s.	n.s.	6.61*(+)

Table 3.15. Two-way classification table (see Table 3.1) derived from the significant bivariate logistic regression models predicting the presence or absence of a Lapwing nesting attempt within a 1km grid square (for renesting data only). Fitted probability estimates varied from 0 to 1 and these were used to predict absence and presence using a series of increasingly stringent thresholds. To assist in model interpretation the percentage of all correctly predicted cases, the percentage of correctly predicted absences, the percentage of correctly predicted presences and Cohen's kappa are given.

		0-0.49:0.5-1.0		0-0.35:0.65-1.0		0-0.2-0.8-1.0	
		Observed (+)	Observed (-)	Observed (+)	Observed (-)	Observed (+)	Observed (-)
Winter cereal+Option 1B	Predicted (+)	9	5	3	1	2	0
	Predicted (-)	8	26	6	22	2	12
	% correct predictions	72.9%		78.1%		87.5%	
	% correct absences	64.3%		75%		100%	
	% correct presences	76.5%		78.6%		85.7%	
	Cohen's kappa	0.39		0.35		0.6	
Option 1B+grass	Predicted (+)	8	4	5	1	4	1
	Predicted (-)	9	27	8	26	1	8
	% correct predictions	72.9%		77.5%		85.7%	
	% correct absences	66.7%		83.3%		80%	
	% correct presences	75%		76.5%		88.9%	
	Cohen's kappa	0.37		0.4		0.46	

3.4 DISCUSSION

3.4.1 1km^2 and field-scale landscape data

It is likely that crop type is a major factor influencing nest-site selection by Lapwings in arable habitats. The proliferation of winter cropping has been well documented and is believed to be one of the primary changes that has negatively effected a wide variety of farmland birds (O'Connor & Shrubb, 1986; Chamberlain *et al.*, 2000), although the underlying causes of agricultural change are underpinned by technological advancements, and one component of agricultural intensification does not proceed independently of another (Chamberlain *et al.*, 2000). The strong avoidance of winter cereals by Lapwing (nationally) has been shown by Shrubb & Lack (1991) and Wilson *et al.* (2001), and indeed this avoidance of winter cropped land has increased over time. In areas dominated by winter cropping nest-site availability may be so scarce as to lead to localised population extinction, this is likely to be exacerbated where high nest loss through predation leads to very few replacement clutches due to advanced crop growth. Furthermore, national surveys have shown areas of spring tillage to be a preferred habitat and are more likely to hold Lapwings than winter crops (Wilson *et al.*, 2001) and this is also true at the local scale (Galbraith, 1988a; Berg *et al.*, 1992; Linsley, 1999).

Lapwings are associated with short, patchy vegetation that is likely to increase nest crypticity. The Arable Stewardship Option 1B prescription was devised with this in mind, and the large numbers of birds that were present on Option 1B is encouraging, as the habitat is believed to mimic fallow conditions favoured pre-intensification (Nicholson, 1938,1939; Lister, 1964).

The habitat-association models that were produced were a poor description of the data, and their predictive power would appear to be weak. Lapwings have two separate components to their habitat requirements during the breeding season, firstly the availability of nesting habitat, and also the provision of chick foraging habitat (for example see Galbraith, 1988a). The modelling procedure adopted does not allow for any spatial element to be incorporated, instead a separate analysis of chick foraging habitat requirements was undertaken (Chapter 5). Furthermore, the semi-colonial nature of the species often leads to 'good quality' fields being unoccupied where

they exist in proximity, as pairs may choose to breed in the same field where collective nest defence may increase the likelihood of nest survival. This is likely to be even more pertinent in areas of low population density, where low numbers of breeding birds increase the likelihood of suitable fields not being occupied. The high levels of site philopatry to natal fields exhibited by the species is an important component of Lapwing breeding ecology which has not been incorporated in to the modelling procedure, a longer study over at least 5 years would ideally be required to incorporate such a variable.

The relationship between Lapwing nest characteristics to landscape variables measured in this study largely follows findings of previous work. The semi-coloniality of Lapwings is clear, but with some clear differences in relation to crop type with the number of active pairs in proximity to nests being highest on 1B and stubbles. This relationship is independent of field size indicating a link to habitat quality. However, territory density as a direct measure of habitat quality can be misleading (Vickery *et al.*, 1992; van Horne, 1993; Donald & Vickery, 2000), as no account is taken of productivity. Indeed, habitats with a high number of birds may act as a sink for some species, with productivity failing to compensate for mortality (McCoy *et al.*, 1999). Somewhat surprising is that on winter crops the density of active pairs in a given field can be quite high despite a general avoidance of the habitat. This would suggest something particular to any given field (see below). Contrastingly, a low number of active pairs are associated with spring tilled fields which are habitats usually strongly preferred by Lapwings, and they also occur at the lowest densities. Hence, although nationally spring tillage is a preferred habitat, there may be some local differences where other landscape features or field specific sward characteristics may be more important.

The distance of Lapwing nests to predator perches and field boundaries is strongly correlated and is unsurprising as many perches are within the boundary. There is an obvious field area effect, with smaller fields (1B, set-aside, grass) being closer to perches and boundaries than larger fields (e.g. winter crops and spring crops). However, distances to predator perches (but not field boundary) differ between nests on winter crops and spring cereals. This would suggest that something specific about winter cropped fields 'forces' them to nest closer to predator perches (see below).

Alternatively, Lapwings may be able to nest closer to predator perches in winter crops due to the more advanced crop growth lending a greater degree of cover and protection than in other crop types. Previous studies have shown this general avoidance of boundary features and potential predator perches (Berg *et al.*, 1992; Linsley, 1999) most likely as part of an anti-predator strategy as Lapwings rely on early sighting of potential predators as a mechanism to avoid nest loss. For winter crops in particular, there appears to be a trade-off between concealment of nests and incubating birds with the requirement for early detection of predators. Wood plots can provide habitat for potential predators of Lapwings (nest and chicks) and these were on average almost 300m away from Lapwing nests. The only nests that were generally close to woods were those on set-aside (and to a lesser degree Option 1B) probably due to the location of such land being more agriculturally unattractive and hence farmers using the more unproductive land to meet set-aside requirements. On such land there is likely to be a trade-off between nest-site availability and nest-site suitability, whereby Lapwings are being 'forced' to take sub-optimal habitats as these are the only nest-sites available.

Although the area of grass was retained in some of the logistic regression models at the $1km^2$ scale, there appears to be little effect of grass habitats which is surprising given the well documented link between nesting fields and proximity to grassland for chick rearing (Galbraith, 1988a), although the density of breeding birds was quite high (Figure 3.7). It may be possible that an effect of proximity to pasture may manifest itself in other demographic parameters such as chick survival. Alternatively, the grass category used here incorporates pasture (improved and unimproved), re-seeded grass and set-aside grass, due to small sample size, and it may be effects would be more apparent if the 'idyllic' unimproved cattle pasture could be separated from other less attractive grassland habitats (see Baines, 1990). Changes in grassland management in recent years have been profound with the conversion of unimproved pasture to improved grassland via increased fertiliser inputs, improved drainage, increased stocking rates, or the switch to intensive silage production. How these changes have affected a wide range of farmland birds is currently receiving much research (Vickery *et al.*, 2000; Perkins *et al.*, 2000; Buckingham, *pers. comm.*), but

the increased sward density and reduced structural diversity probably make many grassland habitats unsuitable as both nesting and foraging habitat.

3.4.2 Fine-scale within field nest-site selection

Many authors have commented on the Lapwings preference for nesting habitat with short and patchy vegetation (Klomp, 1954; Lister, 1964; Kooiker, 1984; Galbraith, 1988a). Liker (1992) showed that Lapwing nests in alkaline grasslands in Hungary had a mean vegetation height of 8.7cm within 1m of the nest which was not significantly different from vegetation 5m from the nest (mean 10.7cm). To my knowledge this is the first attempt to quantify that preference in arable habitats, particularly at the nest level. It was expected to find differences in crop height and cover at nest-sites in different crops due to agronomic differences relating to timing of cultivation and sowing dates. In particular, nests that were found in winter cereals had taller vegetation at the nest-site than did nests that were found in spring sown crops. These differences were more profound when comparing crop cover of winter cereal nests, which were significantly different from all other crop categories. That Lapwings are selecting nest-sites with a maximum crop height of 125mm with a mean figure of 72mm, agrees with what is known of Lapwing habitat use in the non-breeding season. Mason & McDonald (1999) found that Lapwings feeding in winter cereal show a preference for cereal height between 70-110mm but strongly avoided taller cereals, and similar crop height effects during the winter have been found by Gregory (1987) and Village & Westwood (1994). The Lapwing anti-predator strategy of utilising an open landscape to forewarn of approaching predators requires a habitat that will enable a good all round view of the area surrounding the nest. Winter cereal sward structure is generally too tall and dense at the start of the Lapwing breeding season at the end of March, and hence are generally avoided as a nesting habitat. In this study winter cereals were only used by Lapwings at the start of the breeding season when crop height was short, and even then, the fields that were chosen were characterised by a poorly established crop. Furthermore, the nest level data suggests that Lapwing nests on winter cereals are closer to predator perches than they are on spring cereals, despite similarities in field area. This would suggest that crop height in winter cereal is the overriding factor determining nest

placement, assuming that Lapwings will try to optimise nest survival by nesting away from potential predator perches. Such crop height constraints are less relevant in spring cropped fields as most nests are initiated pre-emergence (see below).

The difference in crop cover at the nest-site in winter cereal nests compared to the random measurements was significant prior to adjustment for multiple testing (section 4.2), suggesting that there may also be selection for areas of less crop cover. The non parametric tests used in the analysis of crop cover data are generally less powerful than the parametric equivalents (Sokal & Rohlf, 1995), and from the results of the logistic regression analysis it is apparent that aspects of crop growth had a significant effect on nest placement within winter cereal fields. Shrubb & Lack (1991) suggest that more Lapwings are present in winter cropped fields containing bare patches than would be expected by chance. The presence of patchy vegetation is believed to increase the crypticity of Lapwing nests and hence lessen the chance of predation (Imboden, 1971). Many authors have identified positive effects of nesting success through the selection of heterogenous nest sites (Bowman & Harris, 1980; Osborne & Osborne, 1980; Schieck & Hannon, 1993; Gregg *et al.*, 1994.) The promotion of habitat homogeneity is known to have had negative repercussions on a number of breeding species (Baines, 1988; Grant, 1992).

In spring cereals and other spring cropped fields most nests were initiated on bare ground prior to, or at the very early stages of crop emergence, hence nest-site selection in these fields were likely to be influenced by factors other than crop characteristics. The results show that there are no differences in crop characteristics between within field measurements, and it is likely that nests in spring crops are influenced more by landscape features, such as field boundary composition and distance to predator perches.

It is not surprising that we were unable to produce acceptable crop growth models for set-aside fields as it is widely recognised that the vegetation structure and composition found on naturally regenerating set-aside is generally diverse and varied (Rew *et al.*, 1992). Similarly this is likely to be true for Option 1B, where following spring cultivation vegetation is left to regenerate naturally. Unadjusted vegetation measurements that were used were still adequate for comparison between nest-sites and random measurements within fields. It is somewhat surprising that given the varied

nature of vegetation characteristics on set-aside, differences in nest-site selection were not apparent. It may well be that the inherent heterogeneity associated with set-aside is why Lapwings choose to breed on set-aside, and fine-scale nest-site selection is less important than proximity to other landscape features. Why differences in vegetation height were apparent at the nest site in comparison to random on the Option 1B fields is less clear. It was observed that on many Option 1B fields, particularly following cereals, there was rapid regeneration of vegetation and with Option 1B providing the majority of nesting habitat later in the breeding season, this preference for shorter vegetation becomes more apparent. Further studies are required to address the change in nest-site selection as the season progresses. Temporal scale is likely to be important in nest-site selection particularly in modern agricultural systems where rapid crop establishment will reduce the amount of land suitable for nesting habitat, this is particularly pertinent for a species such as the Lapwing which is dependent on areas of short, patchy vegetation.

This chapter shows that Lapwings are selecting nest-sites with certain characteristics within fields. Whilst nest-site selection at this fine-scale is an important component in addressing factors influencing the breeding ecology of Lapwings, it is important to stress the hierarchical decision making process in which habitat must be found suitable at larger spatial scales before assessment occurs at the next lower level (Speiser & Bosakowski, 1987). At the field level the choice of nest-site is strongly influenced by the presence of certain crop types that cover a certain hectareage, and the relative importance of crop type is likely to increase as the breeding season progresses.

In areas dominated by winter cropping the decision to breed or not may be taken at the field-scale. Due to the Lapwings high site fidelity (Thompson *et al.*, 1994), the nature of within field sward characteristics may be important leading to intraspecific competition for limited nest-sites. In years of good crop growth nest-site availability may be so limited as to lead to localised population extinction.

Height of vegetation in habitat patches (Best, 1978) and spatial heterogeneity (Bowman & Harris, 1980 has been found to be positively associated with clutch success in other ground-nesting birds. Although there were insufficient data to compare successful and unsuccessful nests, it is likely that the differential success of nests influences the evolution of species-typical patterns of nest

placement (Rosenzweig, 1985). Some antipredator activities, such as specialised micro-site nest placement, may be less effective when predation is incidental rather than directed specifically at avian nests (Vickery *et al.*, 1992).

Finally, this chapter shows that Lapwings are able to utilise winter cereal fields where patches of stunted crop growth exist. Recent wet autumns and winters have resulted in many fields in the study area characterised by bare patches due to retarded crop establishment as a consequence of adverse weather conditions. Even so, winter cereals are still generally avoided as a nesting habitat, both at the local scale and at a national scale (Wilson *et al.*, 2001). It is suggested that in areas where winter cropping is dominant, nest-site availability could be limiting and may lead to local declines in breeding Lapwing populations where alternative nest-sites are not available.

The key findings of this chapter are

i) Lapwings select nest-sites within fields, that are characterised by short vegetation and low ground cover

ii) In comparison with other crop types, Option 1B fields held the highest number and density of breeding pairs

iii) Option 1B fields were particularly important for nesting Lapwings laying replacement clutches

iv) Crop type was a major factor influencing Lapwing nest-site selection at a $1km^2$ landscape scale. Winter tillage was generally avoided, and spring cereals and Option 1B had a positive effect on Lapwing nest-site selection

CHAPTER 4

NEST SURVIVAL AND CAUSES OF FAILURE

4.1 INTRODUCTION

The most important factor determining productivity at the scale of the individual nest is nest survival rate (Martin, 1993; Newton, 1993), with total nest failure representing a serious loss of reproductive effort. Reproductive success varies greatly between individuals within a population, and a substantial part of this variation can be attributed to complete breeding failures (Newton, 1989). It is likely that differential success of nests influences the evolution of species-typical patterns of nest placement (Rosenzweig, 1985).

The Lapwing is one of only two widespread farmland bird species that nests solely in open fields avoiding field boundaries (the other being the skylark). As a consequence of this one can expect nest failure rates for the species to be highly susceptible to changes in agricultural management where this impacts on open field habitats, eg cultivations, drilling and chemical applications. Cultivation and harrowing after the start of breeding have been shown to be major factors causing complete failures for Lapwings (Kooiker, 1984; Shrubb, 1990; Berg *et al.*, 1992), although in other studies predation has been the dominant cause of nest loss (Glutz von Blotzheim *et al.*, 1975; Matter, 1982; Galbraith 1988a). Analysis of BTO nest record cards (Shrubb, 1990) show that nests in arable habitats tended to suffer higher nest losses to agricultural operations, and nests in grassland habitats suffered more from predation, although this did vary from study to study. The overall view of nest failure in Lapwings is that losses can be quite significant but the cause varies, although in an arable context losses to mechanical operations are always important and losses to predators can be significant.

Lapwings are known to benefit from breeding in aggregations (Cramp & Simmons, 1983), and survival rates have been shown to increase when breeding in colonies (Elliot, 1982; Berg *et al.*, 1992). Furthermore, the number of close neighbours is also known to have a strong negative effect on daily predation risk (Berg *et al.*, 1992). Predator exclusion by aggressive species such as Lapwings has been shown to have positive nest survival benefits for other ground nesting birds nesting within Lapwing colonies (Eriksson & Gotmark, 1982). Goransson *et al.* (1975) and Elliot (1985) also found evidence to suggest that the presence of nesting Lapwings reduced the rate of

predation on artificial nests in their territories. Conversely, Galbraith (1988a) found no effect of the size of aggregations on predation risk.

Although a wide-range of nest predators are known to predate Lapwing nests, corvids and foxes are generally believed to be the most significant predators. Objects that act as perches for corvids, and linear features that may act as dispersal corridors for foxes may thus be expected to be avoided. Berg *et al.*, (1992) show that nests sites far from trees had a higher survival probability than those near to such perches. Experimental manipulation of predator densities through predator control has been shown to have a positive influence on Lapwing nest survival rates (Pearson & Stoate, 1994).

Recent analyses of BTO nest record cards suggest the pattern of nest survival rates have altered in recent years for Lapwings, with high survival rates around 1980, but a marked decrease in survival rates into the 1990s (Chamberlain & Crick, *In prep.*). However, the observed decline is small and is unlikely to be the driving factor in the recent population decline, particularly when considering the species' ability to re-nest several clutches following initial failure. Even so, any declines in one breeding parameter must be compensated for by an increase in another if the population is to remain stable. It has been shown for some species, such as Corncrake *Crex crex* and Stone Curlew *Burhinus oedicnemus*, that decreases in nest survival rates can drive population declines (Aebischer *et al.*, 2000).

Nest survival has been relatively well-studied in Lapwings and the key causes of nest losses are well known. Furthermore, some of the environmental and landscape factors that may influence those survival rates are also well understood. However, most studies have looked at the effect of one or two variables on nest survival without consideration to other factors likely to influence nest loss. In addition nest survival estimates in arable habitats tend to be investigated in terms of spring and autumn tillage. This chapter aims to

i) determine the main causes of nests loss and to identify differences between crops

ii) identify the key factors that influence nest survival and to identify differences between a wide range of crop categories.

4.2 METHODS

4.2.1 Data collection

Nests were located using the methods outlined in Chapters 2 & 3. Data was collected over two field seasons (1999 & 2000) from the Shropshire study area only. The nest site variables used in this analysis were the same as those outlined in section 3.2.2.

Nests were checked regularly (every 4-10 days) from a distance to obtain information on breeding success and the timing of hatching. If a bird was seen to be incubating then the nest was assumed to be intact. If no incubating behaviour was observed the nest was visited to confirm its status. Nests were checked more frequently nearer the estimated hatch date. On the first check when a nest was found empty, the contents were carefully scrutinised and recorded. Nests were recorded as successful when

i) small fragments of egg shell were present,

ii) at least one chick was seen,

iii) behaviour of the adults indicated the presence of a brood.

A nest was assumed to have failed if it was empty before the expected hatch date (and did not comply with the above criteria), or if there was evidence of predation (i.e. large egg fragments, disturbed nest lining etc.). Nest destruction due to agricultural operations was readily identified by the complete disappearance of the nest. Clutch abandonment was assumed if adults were not seen incubating on two successive visits. Where this was the case one egg was arranged in the scrape with its pointed end facing outwards, if the position of the egg remained the same on the next visit the nest was confirmed as abandoned. Thus nest outcome could be categorised as one of four possible outcomes, successful, predated, loss to agricultural operations, or abandoned; these could be further categorised as two outcomes, success or failure. Nest failure was rarely witnessed as it occurred, and it was assumed to have happened at an intermediate date between the final two visits to the nest scrape. The number of days a nest was observed (exposure days) was calculated from the day the nest was first located through to the day of final nest outcome.

4.2.2 Data analysis

An assessment of nest survival rates simply using the observed proportion of nests that failed or were successful is likely to lead to an overestimation of survival rates. Those nests that are more successful have an inherently greater chance of being located than nests that are lost early in the egg-laying or incubation stages. The standard method for overcoming this potential bias is that proposed by Mayfield (1975), in which nest survival rates are defined in terms of likelihood of failure per day of observation. Daily nest survival rates and hatching success were estimated according to Mayfield (1975), and in an extension of this method a general linear modelling (GLM) procedure was used incorporating a number of variables that may influence nest survival. A binary nest outcome variable (failure or success) was modelled in terms of exposure days to derive an estimate of the daily survival rate. The modelling approach has the considerable advantage over traditional Mayfield methods in that continuous and categorical variables can be added singularly or in combination to allow an assessment of a suite of variables that may add to our knowledge of the mechanisms underpinning nest survival.

Analyses were carried out using GLIM 3.77. The modelling rationale assumed a binomial distribution of errors and a logistic link function was used to relate the binary response variable to the assumed error structure (Crawley, 1993). The exposure period in days was entered as the binomial denominator. A step-up procedure was adopted with each explanatory variable in turn being added to the null model. The reduction in deviance was treated as a likelihood ratio test and its significance assessed by comparing it with the χ^2 distribution at the appropriate degrees of freedom. The explanatory variables used in the analysis of nest survival rates were the same as those used in section 3.2.2.

All significant univariate models were then used to identify significant multi-variate models. The final models therefore included only those terms that had significant independent effects. Traditional methods of hypothesis testing have recently been challenged as uninformative and, of little use in model selection (Anderson *et al.*, 2000). Hence, Akaike Information Criteria (AIC) were used to aid model interpretation. This is calculated as,

AIC = Residual deviance + 2 × (model reduction in degrees of freedom)

One potential problem with nest level analyses is that those nests that are within the same fields are not strictly independent as they are all likely to be influenced by the same factors. The problem of nest level pseudo-replication may artificially inflate the number of degrees of freedom and increase the likelihood of Type 1 errors, consequently a further modelling procedure was adopted to test for this. The response variable became the total number of failures in each field in each year, with the total number of exposure days in that field in that year (failures and successes combined) being entered as the binomial denominator (Donald, 1999). As all nests in each field were combined, continuous variables could no longer be included in the analysis, and only the categorical variables year, region, crop type, boundary index and field area were used.

Overall nest survival rates by crop type were derived from GLM models by assuming a total nesting period of 32 days. This assumes that all nests have four eggs (see Chapter 2.3.1) with two days between the laying of each egg (six days) and a further 26 days to incubate the eggs.

4.3 RESULTS

4.3.1 Causes of nest loss

A total of 188 nests were located, and a large proportion (68%) were recorded as successfully producing at least one chick (Table 4.1). Losses to predation were the main cause of nest failure accounting for 52% of all nest losses (Table 4.1). Nests on grass habitats had a higher proportion of nests predated (88%) when compared to all other crop types (average 55%, range 38%-60%). However, causes of nest loss were not consistent across crop categories (Table 4.1). Losses to agricultural operations were mainly on fields associated with spring tillage, and generally exceeded the number of nests that were lost due to predation. The frequency of nests lost to agricultural operations on spring tillage was more likely than on non-spring tilled fields, where losses to predators were more frequent (Fishers exact χ^2=13.71, P=<0.005, Table 4.1).

The proportion of nests lost to desertion was higher on winter crops (44%) than on any other crop category. There was no significant difference in the number of nests failing due to desertion between winter crops and non-cropped habitats (Fishers exact χ^2=0.73, n.s.) and between all cropped habitats and non-cropped habitats (Fishers exact χ^2=0.86, n.s.).

Table 4.1.The outcome of nests and cause of nest failure by crop category. Figures in parentheses refer to the percentage of nests per crop type that hatched at least one chick or that failed, and is also expressed as the percentage attributable to each of the possible outcomes. Figures in italics refer to the percentage of nests that were lost in respect of the total number of failures for each particular crop type.

Crop category	Success	Total failures	Predation	Agricultural operations	Desertion
Spring cereal	15 (54%)	13 (46%)	5 (18%) *38%*	7 (25%) *54%*	1 (4%) *8%*
Spring crops	28 (76%)	9 (24%)	4 (11%) *44%*	3 (8%) *33%*	2 (5%) *22%*
Stubbles	10 (56%)	8 (44%)	3 (17%) *38%*	5 (28%) *63%*	-
Spring tillage	53 (64%)	30 (36%)	12 (14%) *40%*	15 (18%) *50%*	3 (4%) *10%*
Winter crops	18 (67%)	9 (33%)	5 (19%) *56%*	-	4 (15%) *44%*
Set-aside	18 (67%)	9 (33%)	5 (19%) *56%*	1 (4%) *11%*	3 (11%) *33%*
Option 1B	29 (85%)	5 (15%)	3 (9%) *60%*	-	2 (6%) *40%*
Grass habitats	9 (53%)	8 (47%)	7 (41%) *88%*	-	1 (6%) *13%*
Non spring tillage	74 (70%)	31 (30%)	20 (19%) *65%*	1 (1%) *3%*	10 (10%) *32%*
Overall	127 (68%)	61 (32%)	32 (17%) *52%*	16 (9%) *26%*	13 (7%) *21%*

4.3.2 Factors influencing nest survival

The three significant univariate models for the full dataset (n=188) were the categorical terms crop type and nest status, and distance to field boundary (Table 4.2). A quadratic distance to field boundary term was not significant when added to the linear term (χ^2=1.81, 1 d.f., n.s.). The 'biological' significance of distance to field boundary (likely to be associated with a predator effect) was tested using a reduced dataset (n=159) incorporating those nests that were successful and those that were predated. Both crop type and distance to field boundary were retained as significant univariate models, with the degree of significance increasing for distance to field boundary (Table 4.2). Distance to predator perch is also significant (χ^2=6.61, 1 d.f., P<0.01 (Table 4.2) and is strongly correlated with distance to field boundary (Pearson r=0.72, P=<0.05). Nest status was no longer significant in the analysis of those nests that were successful and lost to predation only.

Table 4.2. Significant univariate models shown to influence nest survival. The all nest column includes those nests that failed and all successes (n=188), and the predated column includes only those nests that were lost to predation and all successes (n=159). Significant χ^2 are given with the associated degrees of significance, *=P<0.05, **=P<0.01. The sign of the parameter estimate is given in parentheses. D.F.B.=distance to nearest field boundary, D.P.P.=distance to nearest predator perch.

Explanatory variable	d.f.	χ^2 (all nests)	χ^2 (predated)
Crop	6	17.78**	12.65*
Nest status	1	4.39*	n.s.
D.F.B.	1	5.22*(+)	6.77**(+)
D.P.P.	1	n.s.	6.61**(+)

The most parsimonious multivariate model, i.e. that with the lowest AIC, for the whole dataset is that which includes the categorical crop variable and its interaction term with distance to field boundary (χ^2=40.08, 13 d.f., P<0.001, Table 4.3). The significance of the interaction term suggesting that the parameters 'behave' differently when combined in different pairings. The slope of survival of one crop type is slightly different to that of another with respect to distance, although the direction is the same for both. Also note that crop type could not be combined with the nest status variable suggesting that there are systematic differences in nest survival or causes of nest loss in relation to nest status on certain crops (Tables 4.1 & 4.3).

For the reduced dataset incorporating only those nests lost to predators, the most parsimonious model is that including the crop term and distance to predator perch (χ^2=22.87, 7 d.f., P<0.01, Table 4.3). The highly correlated nature of distance to field boundary and predator perch does not allow them to be included in the same model. The significance of the interaction terms again suggests that the direction of the slope is in the same direction but the effect with distance is different between crops. No quadratic terms could be retained in the model for either of the distance variables.

Table 4.3. All significant multi-variate models of nest survival compiled from the significant univariate models outlined in Table 4.2. For each model the total reduction in deviance is given compared with the χ^2 distribution and its associated significance, **P*<0.05, ***P*<0.01, ****P*<0.001. The Akaike Information Criteria (AIC) is given to aid model selection, the best model for each dataset is that with the lowest AIC and is highlighted in bold. It should be noted that AICs can not be used to compare models from the two different datasets as the sample sizes are not equal. DFB=distance to nearest field boundary, DPP=distance to nearest predator perch.

Crop	Nest status	DFB	DPP	Crop.DFB	Crop.DPP	df	χ^2	AIC	Farm (17df)
All (188 cases)									
				✓	na	7	26.32***	212.46	24.1
✓				✓	**na**	**13**	**40.08*** **	**210.7**	27.59*
✓		✓			na	7	26.72***	212.06	22.37
	✓	✓			na	2	10.12**	218.66	22.82
Predated (159 cases)									
	na				✓	7	17.87*	150.45	15.35
	na			✓		7	18.98**	149.3	19.02
✓	na	✓				7	21.97**	146.36	18.45
✓	**na**		✓			7	**22.87****	**145.45**	15.27
✓	na			✓		13	33.31**	147.02	18.45
✓	na				✓	13	30.12**	150.21	15.7

Daily nest failure rates estimated from the parameters of the models for each crop category and for nest status are given in Table 4.4. Field level estimates are broadly similar to nest level estimates with the exception of those nests associated with stubble fields (Table 4.4) suggesting that there is some level of pseudo-replication between nests on stubble fields and factors affecting nest survival are not independent between such nests.

Table 4.4 Daily nest survival rates derived from GLMs with associated overall survival for the whole nesting period (P^{32}). The data is presented for both nest level analyses (n=188) and for field level analyses (n=61), see text for details.

		Nest level estimates			Field level estimates		
Variable	Category	n	P	P^{32}	n	P	P^{32}
Crop	W/crop	27	0.9815	0.5498	10	0.9815	0.5498
	Spr/cer	28	0.9596	0.2674	13	0.9585	0.2572
	Spr/crop	37	0.9847	0.6106	14	0.9803	0.5296
	Sas	27	0.9767	0.4707	8	0.9767	0.4707
	1B	34	0.9915	0.7606	5	0.9897	0.7189
	Stubbles	18	0.9612	0.2819	5	0.9767	0.4707
	Grass	17	0.9551	0.2295	6	0.9551	0.2295
Nest status	First nest	136	0.9742	0.4335			
	Replacement	52	0.9865	0.6473			

Nests that were greater than 50m distant from a field boundary had a better chance of survival than nests that were less than 50m away (χ^2=7.72, 1 d.f., P<0.01, Figure 4.1), irrespective of crop type. An improved chance of survival was also found for nests that were greater than 50m distant from the nearest predator perch (χ^2=5.19, 1 d.f., P<0.05).

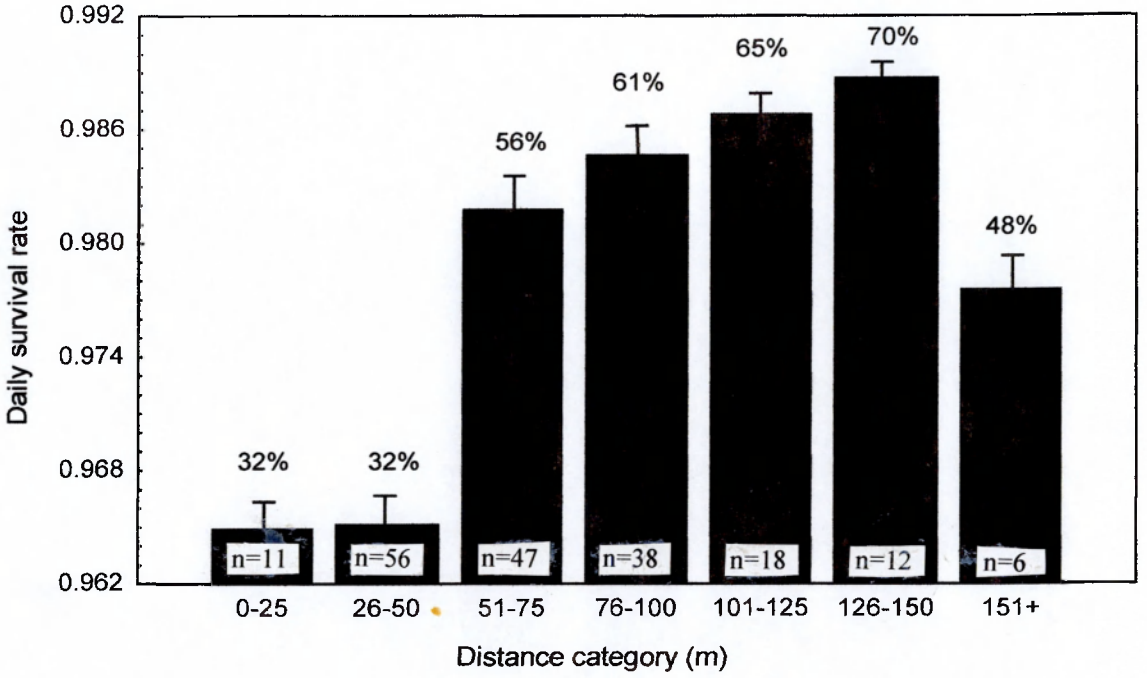

Figure 4.1. Daily nest survival rates derived from GLM estimates in relation to distance categories from the nearest field boundary. The percentage figure above each bar refers to the overall survival rate (P) over the whole nesting period (P^{32}). Nests <=50m had a greater chance of survival than those >50m distant from a field boundary (χ^2=7.72, 1 d.f., P<0.01). Error bars denote one standard error.

4.4 DISCUSSION.

4.4.1 Causes of nest failure

A large proportion of nests in this study were successful in that they hatched at least one chick. However, of those nests that failed to hatch any young the most common cause of nest failure was predation followed by losses to agricultural operations. The relative importance of these tends to vary from study to study, usually due to underlying differences in predation pressure and landscape composition. Galbraith (1988a) showed nest loss to predators to be high accounting for about 75% of nest losses, but with differences across habitats, and similar findings have been reported by Matter (1982) and Baines (1990). In contrast, in a study in North West England, Linsley (1999) showed that of all nests that failed, loss to predators were less than 15%, but this was almost certainly due to a reduction in pressure through heavy predator control. However, in the same study losses to agricultural operations were high and this varied across crop types, with spring tilled fields losing more nests to farm operations than other fields with set-aside or winter crops. This was further highlighted by the high loss of nests on unsown fields (56%) compared to sown fields (5%) (Linsley, 1999). Similarly, Berg *et al.* (1992) show nest loss due to predation to be relatively low (14%) with an increasing importance of farming operations influencing nest loss. The relative influence of agricultural operations on nest loss will vary greatly from study to study depending on the dominating habitat and the associated cultivation period. Losses to agricultural operations in this study were few but were more prevalent on certain crop categories, with most losses on spring cereals and stubbles. Losses to rolling were observed on spring cereals and ploughing accounted for most nest losses on stubble fields. No measure of predation pressure was undertaken in this study but predator control is known to be undertaken on most farms, although the intensity varied greatly. However, losses to predators were similar across all crop types, with the exception of grass fields where nest loss to predators was high. There is some evidence to suggest that grass fields are a preferred habitat for corvids (Henderson *et al.*, 2000), and could be a possible explanation for a reduced nest survival rate associated with such fields (assuming that corvids are the major predator). Other studies of grassland habitats have shown nest loss to

predators to be important (Galbraith, 1988a; Baines, 1990; Shrubb 1990). Although grass fields in this study were not divided into improved and unimproved, most of the fields were temporary grass leys, with a relatively uniform sward structure. Baines (1990) argues that the uniform nature of the sward structure associated with improved grassland explained the observed high nest loss to avian predators, due to a lack of nest crypticity. Nest crypticity has been shown to enhance nest survival in Whimbrel *Numenius phaeopus* with fewer nests lost to predators in hummock-bog habitat compared to nests that were in more uniform habitats (Skeel, 1983). Furthermore, work on other species has shown that by reducing predation pressure through legal predator control can lead to increased hatching success (Duebbert & Lokemoen, 1980; Parker, 1984; Potts, 1986). However, in their meta-analysis of published literature on predator control programmes for bird conservation, Côté & Sutherland (1995) concluded that predator control does not result in an increase in breeding bird populations.

The only other common British farmland bird that utilises open field habitats for nesting is the skylark, and the majority of nest failures are known to be caused by predation (Donald, 1999). Stone curlews that breed on spring tillage are susceptible to nest loss by agricultural operations, but breeding success on arable farmland has improved by 35% where preventative measures have been implemented (Aebischer *et al.*, 2000). Similarly, corncrake declines largely driven by reduced nest survival since the introduction of mechanised mowing have been ameliorated since the introduction of both voluntary schemes and direct compensation payments to farmers (Green, 1995; Williams *et al.*, 1997: Tyler *et al.*, 1998; Aebischer *et al.*, 2000).

4.4.2 Factors affecting nest survival rates

In this study, despite losses of nests to both predators and agricultural operations, actual nest survival as expressed in terms of daily survival rates were generally high in comparison with other Lapwing studies (Table 1.7). Furthermore, Lapwing nest failure rates have remained fairly stable over the period of recorded population decline, although there has been a suggestion of a small decrease in survival rates probably as a consequence of trampling effects by livestock on grassland habitats (Chamberlain & Crick, *In prep.*); furthermore, an increase in losses to predation is likely

to have been mediated by changes in habitat conditions through increased grazing and pasture improvement.

However, there are clear differences between crop types, with nest survival on spring cereals, stubbles and grass habitats being very low. Much of this can be explained by nest loss on the arable fields being driven by losses to agricultural operations, and increased predation pressure on grass fields. This is further highlighted by lower overall survival rates for first nesting attempts, in comparison with re-nests, which coincides with the period of most intense agricultural operations.

The high survival rate on Option 1B fields is one of the highest recorded in the literature (Table 1.7). Lapwings nesting on Option 1B fields tended to breed in association with other Lapwings, at high density and in closer proximity to neighbours in comparison to other crop types (Table 3.9 and Figure 3.7). Although increased survival benefits from breeding in aggregations and at high densities have been shown in other studies (Elliot, 1982; Berg *et al.*, 1992) there is no evidence from the models generated in this study to suggest that this is the case for Option 1B. This would suggest that something more specific about Option 1B fields influences nest survival rates, and may be explained by increased habitat heterogeneity associated with such fields (Figure 3.2). The best multivariate model (for all nests) suggests that crop type and the interaction term with distance to field boundary explains the largest amount of the variation in survival rates. If heterogeneity and/or the amount of cover affords any benefit in terms of nest survival for Lapwings, this will likely increase with distance from the field boundary. The amount of crop cover and heterogeneity differs across crop type and this may go some way to explaining the high survival rate on Option 1B fields. The hypothesis that increased crop cover and/or heterogeneity offers protection against predation seems more pertinent for Option 1B as these fields were generally smaller and thus closer to boundary features, and arguably more susceptible to predation. Donald (1999) suggested that skylark nests in cereals for example were built under significantly higher vegetation than other habitat types, possibly providing better cover and protection from predators. One would expect this benefit to increase with distance from predator perches. The structure of vegetation at nest sites varies according to crop type (Chapter 3.3.1) and in other

species this has been shown to have an effect on survival rates (Kyrkos, 1997; Hughes *et al.*, 1999).

However, analyses of successful and predated nests only suggests that the best multi-variate model is that which included crop type and distance to predator perch. The lack of an interaction effect with crop type suggests that cover no longer affords protection, although significant models were produced with interaction terms (Table 4.3). The contrasting results between the two datasets seem to be contradictory, but the relatively high survival rate may have masked any effects that the measured variables may have. If predation rates in particular had been higher, those variables associated with nest survival may have shown a greater response in the analyses. Even so, distance to the nearest field boundary and predator perch do seem to be associated with a predator effect. Furthermore, the results suggest that a simple management tool to mediate predation effects would be to target Lapwing habitat provision in areas that are at least 50m away from such features (Figure 4.1). The lack of any significant effect of nest status in the reduced dataset would suggest that predation pressure is constant throughout the nesting period, but losses to agricultural operations are only significant early in the breeding season.

GLIM survival estimates from field level analyses are broadly similar to the nest level analyses, suggesting that the treatment of each individual nest as independent from others in the same field is credible. The exception are those nests in stubble fields which are generally lost to agricultural operations, hence all nests are likely to be lost at once and as such are not independent. Similarly, it was rare for predators to be identifiable with any degree of certainty from signs left at the nest, so the relative importance of predator type cannot be assessed directly. However, as mammalian nest predators, such as foxes, detect nests by olfactory cues the location of one nest within a field is likely to lead to the detection of another, and thus would not be independent. The similarity of nest and field level estimates would suggest that the principal predator would be avian predators, such as corvids, which rely on visual cues to locate nests.

The key findings from this chapter are

i) The most common causes of nest failure were predation and losses to agricultural operations. Losses to agricultural operations were the main cause of nest loss on spring cereals and stubbles

ii) Crop type and the distance to the nearest field boundary were shown to influence nest survival

iii) Lapwing nests that were greater than 50m distant from a field boundary had a better chance of survival than nests that were less than 50m away.

CHAPTER 5

CHICK GROWTH, CONDITION, SURVIVAL AND FORAGING BEHAVIOUR

5.1 INTRODUCTION

Lapwings nest in a wide range of habitats but, are often strongly associated with mixed farming as they require spring-tilled arable fields for nesting, and invertebrate rich pasture for chick rearing (Wilson *et al.*, 2001). A number of studies have suggested that the recent population decline in Lapwings is due to poor breeding productivity (Hudson *et al.* 1994; Peach *et al.* 1994; Linsley 1999). A review of 23 recent Lapwing studies shows that only 9 attained a breeding productivity level sufficient to maintain population stability (Table 1.7). Furthermore, of eight arable populations only two studies (Beser & Helden-Sarnowski, 1982; van Impe, 1988) achieved sufficient breeding productivity levels to maintain population stability. Overall breeding productivity is a function of egg survival, re-laying, and chick survival. The most sensitive of these is likely to be chick survival because losses can not be compensated for.

Chick survival has been reasonably well-studied in Lapwings but analyses have tended to focus on comparisons between chick survival rates on arable land and grassland habitats (Galbraith 1988a; Baines 1989). Furthermore, previous studies of chick survival have primarily utilised re-sighting and/or re-capture of metal ringed individuals to determine survival. Use of these methods to determine chick survival are often inaccurate. For grassland habitats a number of studies have investigated specific mechanisms that effect Lapwing chick survival. Baines (1989) showed that Lapwings breeding on agriculturally improved pasture had lower fledging success and chick productivity than Lapwings breeding on unimproved grassland. Improved fields were characterised by high levels of fertilisation, low water tables and regular ploughing and re-seeding, which resulted in a uniform sward and increased grass yields and livestock carrying capacity. Recent changes in grassland management have been shown to have affected nesting phenology in The Netherlands, with Lapwings nesting approximately two weeks earlier than they were at the start of the twentieth century (Beintema *et al.* 1985). Although, the subsequent effects on chick survival were not studied, negative effects on chick survival would have counteracted an evolutionary response to earlier nesting.

Factors that affect chick survival in arable landscapes are generally poorly understood, particularly in the context of crop use. Changes in arable cropping patterns in recent years have been dramatic (Chamberlain *et al.* 2000), but in recent Lapwing research, little attention has been given to how these may have affected chick survival. The polarisation of farming systems, with the concentration of arable cropping in the south and east, and livestock in the north and west, and the subsequent decline of mixed farming may well have had a negative effect on chick survival and thus breeding productivity. Galbraith (1988a) and Blomqvist & Johansson (1995) showed that chicks with access to pasture survived better than chicks that had to move greater distances. Spring tilled fields are known to be preferentially selected if they abut grassland (Wilson *et al.* 2001). Similarly, Redfern (1982) showed that chicks hatched on blanket bog were moved to nearby invertebrate rich pasture to forage, although no negative effects of chick movement were reported.

Furthermore rapid crop growth may limit available foraging habitat and increase the need for chick movement between fields, which may lead to an increased risk of starvation and/or predation. Linsley (1999) reported higher chick mortality in years when advanced crop growth caused chicks to move from natal fields to suitable chick rearing habitat. Similarly, Galbraith (1988) showed that in years of retarded crop growth, chicks remain on natal fields. However, neither Linsley or Galbraith quantify what is the maximum crop height or structure which Lapwings are able to tolerate before being forced to seek alternative chick rearing habitat.

In a number of bird species, including Lapwing, larger eggs are known to produce larger chicks (Byrkjedal & Kålås 1985, Galbraith 1988b, Thompson *et al*, 1990; Grant 1991). The survival of Lapwing chicks, up until ten days after hatching, has been shown to be positively influenced by egg size (Galbraith 1988b; Hegyi, 1996; Blomqvist *et al*, 1997; Linsley 1999). However, there is no evidence to suggest that Lapwing egg size has declined during the period of population decline (see Chapter 2).

Chick condition indices (i.e. the relationship between bill-length and body weight) and growth rates have been shown to be correlated with rainfall in May (Beintema 1994). There was no direct evidence between chick condition indices and chick survival. Other studies have highlighted the impact of prevailing weather conditions on growth and survival of both Lapwings and other

precocial wader species (Pienkowski 1984; Beintema & Visser, 1989a, 1989b; Beintema 1994). However, there is no evidence to suggest that the current population decline is in response to shifts in weather patterns.

The aims of this chapter are to:

1) quantify chick survival.
2) identify determinants of chick growth and condition.
3) investigate temporal variation in crop use by broods, and to quantify movements between crop types.

5.2 METHODS

Using the methods outlined in Chapter 2, it was possible to calculate the approximate expected hatching date of each nest. Nests were visited on the expected hatch date to enable the whole brood of chicks to be ringed whilst in, or near (<2m) to, the nest scrape. Chicks located in the scrape were treated as having hatched that day, and were thus chicks of a known age (ie 0 days old). Furthermore, chicks that were found on the day of hatching were used to assess the relationship between mean egg volume (see Chapter 2) and chick weight at hatching. Each chick was ringed with a BTO metal ring, size D2 (Redfern & Clark, 2001), on the left leg with a unique reference number allowing individual identification upon re-capture. If chicks were found out of the scrape, ie because they had hatched early, they were treated in the same manner as above, but their age was estimated from growth curves derived from known age chicks. After leaving the nest scrape, chicks were not necessarily located in the immediate vicinity of other chicks in the same brood. Where this was the case, on finding the initial chick the surrounding area was carefully and systematically searched by walking parallel lines (about 2m apart) to the left and right of the chick until other chicks (if any) were located. The search area was approximately 10m in all directions of the focal chick. However, this distance increased to about 50m in all directions when the chicks were near fledging age. Alternatively, if two fieldworkers were working together, one fieldworker

would maintain visual contact with the chicks (using a telescope) for as long as possible and guide the second fieldworker to the vicinity of the last known chick location. This greatly facilitated the ease in which chicks were located. All chicks were weighed and measured for bill length. Small chicks of approximately 10 days or younger, had a habit of freezing in a crouched position, and could be weighed easily by placing in a plastic dish on an electronic balance accurate to 0.1g. Larger chicks (chicks older than 10 days) had to be weighed in a ringing bag using a Pesola spring balance accurate to 0.5g. Bill measurements were taken from the bill tip to the start of the feathering at the base of the bill using dial callipers accurate to 0.1mm.

Depending on time constraints of other fieldwork, chicks were generally recaptured after 7 days for colour-ringing with a unique combination of five plastic colour rings. This enabled individual identification of chicks in the field without the need for re-capture. However, colour-ringed chicks were still caught regularly (every 4-28 days) where possible, to enable further biometric measurements to be taken. These additional measurements were taken to enable the calculation of growth curves.

5.2.1 Radio-tracking

The reliance on visual re-location of chicks using colour rings may lead to habitat related bias due to difficulty of sighting chicks in, for example, tall crops or ditches. Furthermore, in 1999 it was found that visual relocation and positive identification of individual colour-ringed chicks could take in excess of one hour, and was thus very time consuming.

Radio transmitters were attached to chicks in 1999 (Cambridge only) and 2000 (Shropshire only). Holohill LB-2 transmitters were used weighing 0.6g and with a battery life of 21 days. The approximate detection range was 1km depending upon the nature of the terrain.

Each individual transmitter was glued (using epoxy resin) to an oval piece of cotton gauze about 50% larger in length and breadth than the transmitter body. Prior to attachment to the chick the cotton gauze mount and the dorsal surface of the transmitter were daubed with a permanent black marker pen to minimise the risk of detection by predators. These procedures were carried out prior to daily fieldwork, hence minimising chick handling time. Only one chick per brood was radio-

tagged at any one time, and the chick selected was the first one to be removed from the ringing bag (ie randomly). The transmitter and mount was attached to the central position of the back of the chick with 'Copydex' glue. This method has been used for adult Corncrake with no apparent long-term effect (Tyler *et al.* 1996). The total weight of the transmitter, mount and gauze was approximately 1.0g. Most 0 day old chicks weighed about 17g (estimated from measurements of 165 chicks) making the increase in load about 6%, within the 4-6% load increase limit as proposed by Kenward (1987). Furthermore, recent research into the effects of radio tagging on weight gain and survival of curlew chicks showed not detrimental effects of tag attachment (Grant, 2002). Tagged chicks were relocated and recaptured within 48 hours (usually within 24 hours) to ensure the tag was properly attached and to ensure there were no obvious ill effects of tag attachment. Chicks were tracked using a Yagi antenna and a TR-4 radio receiver to ascertain field use and establish if the chick was alive or dead; chicks were checked from a distance every two days. When re-locating chicks, the field where the chick had been previously located was checked initially. When chicks were located alive (the degree of fluctuation of the strength of the signal allows an assessment of whether the chick is moving or inactive) they were observed from a distance to avoid disturbance and to allow a visual assessment of brood size. Approximately every 5-7 days chicks were recaptured and biometrics were taken to further growth studies. If no signal was detected, all adjacent fields up to a distance of 1km from the previous chick location were searched. If there was still no signal the chick was assumed missing. Missing chicks were searched for on two further occasions and if they were still missing they were assumed dead. On no occasion when a chick was assumed missing were they relocated at a later date. Tags can often emit signals post chick mortality and the corpse recovered. This may give an indication of how the chick died, and, where relevant, the nature of the predator.

Chicks that were radio-tagged were still captured and fitted with colour rings to enable individual identification once the radio tag batteries had drained. Furthermore, observations of fledged birds in post breeding flocks and in subsequent breeding seasons may provide further knowledge on post fledging survival and movements, and site philopatry and recruitment rates.

5.2.2 Growth curves

Growth curves were fitted separately to weight and bill length measurements of known age chicks to enable chicks of unknown origin to be aged. The standard curve fitting procedure of GENSTAT was used, which enables a variety of growth curves to be fitted to each dataset. Linear, exponential (asymptotic), logistic and Gompertz curves were fitted to the data. The curve that gave the least amount of residual variation was taken as the curve of best fit. Chicks of unknown origin could be aged by entering either weight or bill length into the appropriate curve equation, or visually by reading off the axis of the relevant graphical plot.

5.2.3 Chick growth rates

Chick growth rate was estimated for chicks for which there were biometric data at least 2 days apart. The mean daily growth rate (g/day) was calculated for each individual chick using the equation:

observed weight (day 2) – observed weight (day 1) / number of interval days

Consecutive measurements were used to calculate mean daily growth rates, and in many instances chicks had more than one estimate. Where this was the case the average mean daily growth rate was calculated for each individual chick. Furthermore, to avoid non-independence of data and pseudo-replication the average mean daily growth rate per brood was calculated (chicks from the same brood were likely to exhibit similar growth rates). Measurements used in analyses were those taken from the linear portion of the growth curve, from day 7 until day 28 (see Figure 5.4).

5.2.3.1 *Data analysis*

GLIM 3.77 was used to model brood daily growth rate (g/day) using normal errors and an identity link (Crawley, 1993). Mean egg volume, hatch day, average brood condition, and average soil moisture deficit for the relevant period were treated as continuous variables, and a 5-level categorical crop type variable was used to describe the crop type that measurements were taken on.

The maximal model was fitted and all explanatory variables were deleted in turn to assess the significance of the term in respect to the reduction in deviance. The variable explaining the least amount of deviance was dropped if it was non-significant. The only terms left in the final model were significant. Quadratic terms were also fitted to detect non-linear relationships with the response variable (ie growth rate). The goodness of fit of the final models were assessed by plotting standardised residuals against the standard normal cumulative distribution function using the MCHECK macro of Crawley (1993).

5.2.4 Chick condition

Standardised chick weights calculated by Beintema (1994) have been used in previous RSPB Lapwing research to ascertain chick condition indices. However, on The Ouse Washes, even in years of poor chick productivity, mean chick condition was greater than average, ie >1.0 (Tyler *pers. comm.*). This suggests that standardised weights on which the indices are calculated from other studies, in other locations, may not be applicable to other datasets. Furthermore, Beintema (1994) noted that chick condition was influenced by rainfall, and are therefore likely to be affected by soil moisture deficit (SMD).

A dataset conforming to the following criteria were used to calculate the relationship of bill length to weight, from which standardised weights could be established specific to the Shropshire study area:

i) chicks must be of a known age,

ii) biometrics must have been taken during a period when SMD did not exceed 9.9mm.

Individual body condition indices (BCIs) were then calculated using the equation:

BCI = observed weight / standardised weight

Hence, chicks with a BCI >1.0 were deemed to be in good condition, and <1.0 were in poor condition.

For chicks with more than one BCI value an average was taken to prevent any non-independence of data in further analyses. Similarly, where analytically appropriate a mean brood BCI was used to prevent possible pseudo-replication (chicks from the same brood are likely to have similar BCIs).

5.2.4.1 *Data analysis*

Mean brood BCIs were modelled using normal errors and an identity link. Date of hatching, crop specific SMD (continuous variables) and crop type (categorical variable, 5-levels; winter crops, spring crops, set-aside, grass and Option 1B) were included in the maximal model with quadratic and two-way interaction terms. All explanatory variables were deleted in turn to assess the significance of the term in respect to the reduction in deviance. The variable explaining the least amount of deviance was dropped if it was non-significant. The only terms left in the final model were significant. The goodness of fit of the final models were assessed by plotting standardised residuals against the standard normal cumulative distribution function using the MCHECK macro of Crawley (1993).

5.2.5 Chick survival

Chick survival was determined either by:

i) actual relocation of chicks during capture for ringing, colour ringing and the taking of biometrics,

ii) visual observation of colour ringed chicks from a distance,

iii) detection of signals from radio tagged chicks (see 5.2.1)

Chicks were relocated by checking the fields in which they were previously recorded. If no chicks or adults were seen to be present, adjacent fields up to a distance of 1km were searched, if chicks were still not relocated they were assumed missing. Missing chicks were searched for on two

further occasions, if they were still missing they were assumed dead. Chicks were observed until they either died or fledged, usually 35 days.

In Shropshire 1999 chick survival estimates were derived from the relocation of metal and colour ringed chicks only. In Cambridge 1999 and Shropshire 2000 survival estimates were derived separately, i) from radio tracking data, ii) metal/colour ringed chicks.

5.2.5.1 *Data analysis*

Chick survival of radio tagged chicks was analysed using GLIM 3.77, with a binomial error distribution and logit link function specified. Only one chick per brood was tagged at any one time, and chicks were thus treated as independent and adopted as the unit of analysis. For each chick day a fate was determined, whereby 0=alive, and 1=dead. The independent variables crop category (6 level factor of grass, set-aside, winter crops, spring cereal, other spring crops, and Option 1B), mean egg volume, chick age, chick condition, date and soil moisture deficit were added and then deleted to the null model. The reduction in deviance was treated as a likelihood ratio test and its significance assessed by comparing it with the χ^2 distribution at the appropriate degrees of freedom.

5.2.6 Chick productivity estimates

Chick productivity estimates are expressed as the number of chicks fledged per female per year. Adult Lapwings were not individually recognisable and hence productivity estimates are either a maximum or minimum estimate. Maximum and minimum productivity per female can be estimated by assuming that all replacement clutches in any one field are from the same females that laid first clutches (maximum productivity), or subsequent re-nesting attempts are from different females (minimum productivity).

An alternative measure of productivity would be to combine mean clutch size (chapter 2), nest survival (chapter 4) and chick survival to give a number of fledged young produced per female:

$$\text{Productivity} = C \times NS + (1 - NS(C \times NS \times CS)) \times CS$$

Where, C=mean clutch size, NS= nest survival rate, and CS=chick survival rate. Pairs that fail at the first attempt are assumed to all re-nest once. Using the data on nest survival rates from Table 4.4 (Chapter 4) an estimate of crop-specific breeding productivity can be made.

The breeding productivity estimates generated in this study must be treated with a degree of caution due to some underlying assumptions that are made about re-nesting behaviour. The assumption that all birds will re-nest once is not strictly true as there are likely to be habitat constraints (increased crop growth in winter crops for example) which would prevent a proportion of birds laying replacement clutches. However, to counter this, where replacement clutches fail, there will be a proportion of birds that will lay a third clutch (this was thought to have occurred on at least two separate occasions). Robust assumptions regarding re-nesting behaviour of Lapwings can only be achieved through marked individuals, and at present there exists no suitable method to mark adult Lapwings in the breeding season, without potentially affecting their subsequent behaviour.

5.2.7 Foraging-habitat associations and chick movements

Whenever chicks were relocated the crop type and OS grid reference were recorded. This enabled an investigation into temporal changes in chick habitat associations. In 1999 (Shropshire data only) the percentage of individual chicks in a given crop category on each day was estimated. If a chick moved between crop types between visits, the date of change was taken as the intermediate date. Similarly, if a chick was not relocated the date of mortality was assumed to be the intermediate date. Using individual chicks as the 'sampling unit' may lead to non-independence of data, but this was necessary in 1999 due to small sample size. However, this dataset was plotted graphically to allow a visual assessment of temporal changes in crop use, and was not subject to further statistical analysis. In 2000, a more comprehensive dataset allowed individual broods to be treated as the sampling unit.

To investigate chick dispersal, approximate straight-line distances that chicks moved were estimated from the centre of the natal field to the centre of the field of relocation using 1:25000 OS

maps for both the Cambridge and Shropshire datasets. A subset of this data using only radio-tagged chick relocations were used to estimate differences in movements between crop categories. Radio-tagged chicks were usually checked every 2 days allowing an accurate assessment of time and distance of movements. The rate of movement was calculated by measuring the distance (m) between successive locations and dividing by the time (days) between them, and was expressed in m/day. Movements between crop types are compared by assigning the rate of movement to the crop that the chick dispersed from.

5.3 RESULTS

5.3.1 Mean egg volume and chick weight at hatching

Measurements of mean egg volume and corresponding mean chick weight from 46 clutches/broods (Shropshire only) showed a strong positive relationship (r=0.76, P<0.001; Figure 5.1). Furthermore, there was a positive relationship between mean egg volume and mean brood condition index at hatching (r=0.6, P=<0.001; Figure 5.2). The body condition of very young chicks is therefore likely to be influenced by the size of the egg from which it hatched. Chicks less than two days old are unlikely to be influenced by external food availability, as until that age yolk sac material is still being digested. In all further analyses of chick condition and weight, chicks less than four days old were excluded.

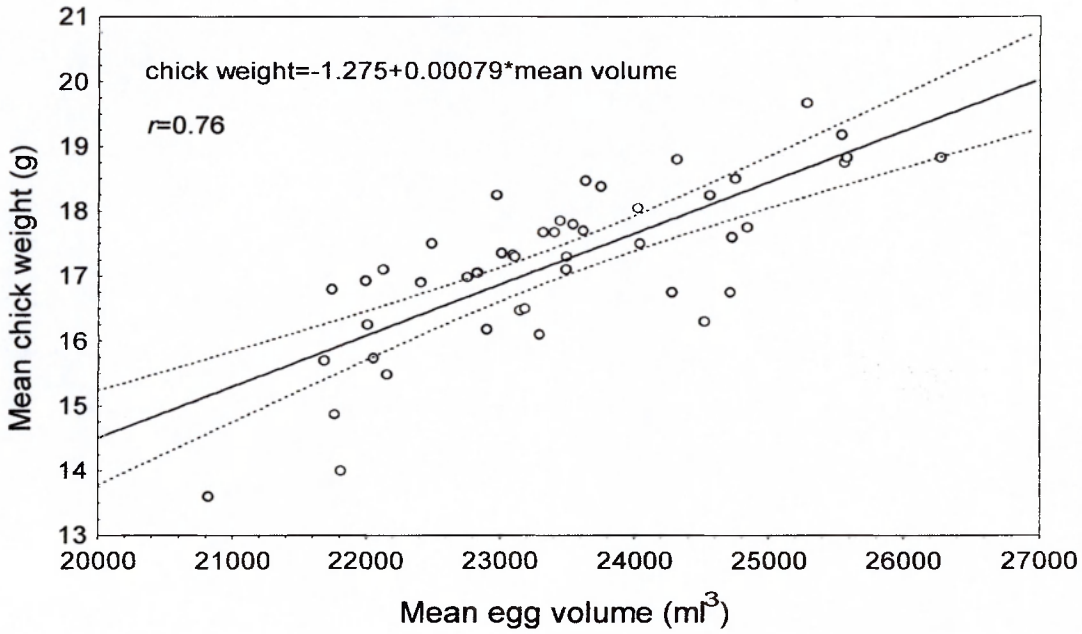

Figure 5.1 Correlation between mean egg volume versus mean chick weight at hatching. The solid line represents the fitted regression model, with 95% confidence limits (dashed lines).

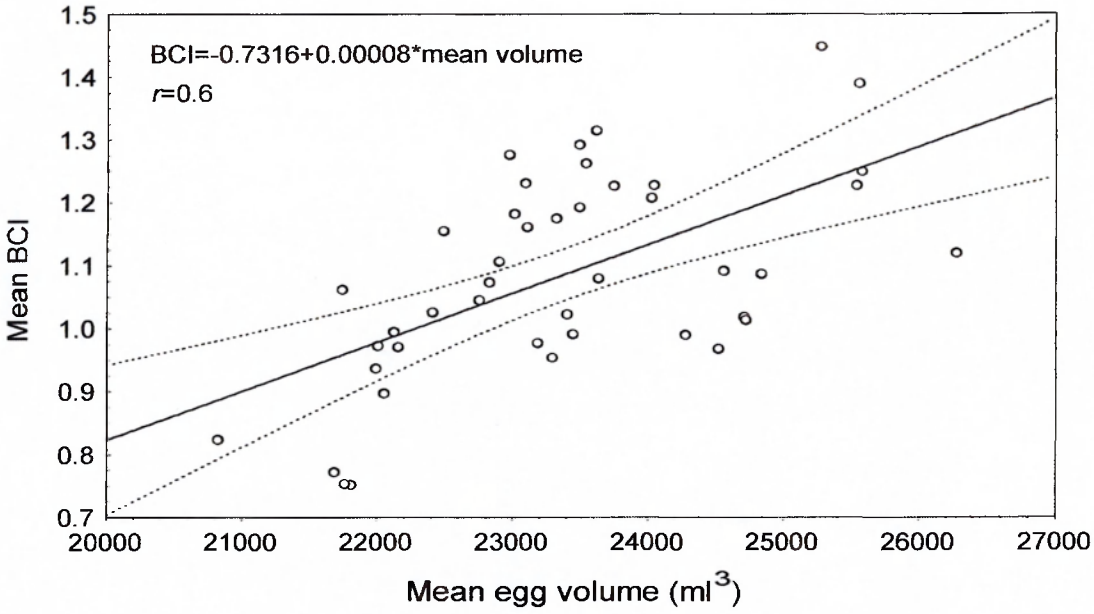

Figure 5.2 Correlation between mean egg volume versus mean chick body condition index at hatching. The solid line represents the fitted regression model, with 95% confidence limits (dashed lines).

Table 5.1. A summary of the number of chicks known to have hatched and the number of chicks that were metal ringed, colour ringed and radio tagged.

	BROODS OF KNOWN NEST OF ORIGIN				UNKNOWN BROODS		
Study area & Year	Total chicks hatched	Total chicks metal ringed	Total chicks colour ringed	Total chicks radio tagged	Total chicks metal ringed	Total chicks colour ringed	Total chicks radio tagged
Cambridge 1999	149	100	29	11	71	35	6
Shropshire 1999	115	55	35	-	-	-	-
Shropshire 2000	319	254	57	43	47	22	8
TOTAL	583	409	121	54	118	57	14

A total of 527 chicks were individually metal ringed during the two years of data collection from both study areas. Of these a further 178 were colour ringed, and a further 68 fitted with radio transmitters (Table 5.1).

5.3.2 Chick growth curves

Only data collected from the Shropshire study area is used in the calculation of chick growth curves. A total of 145 individual chick measurements taken from times of low SMD (<9.9mm) were used in the curve fitting process. A Gompertz growth curve gave the best fit to the bill length data:

$$Y=A(\exp(-\exp(-K(\text{age}-t)))) \qquad Y=23.67(\exp(-\exp(-0.086(\text{age}-5.08))))$$

Where Y is the measured bill length (mm), A is the asymptote, K is the growth coefficient, and t is the time of inflexion.

The fitted curve accounted for 95.5% of the variance and is plotted graphically in Figure 5.3.

This model was used to recalculate the age of chicks from unknown broods.

A logistic growth curve gave the best fit to the chick weight data:

$$Y=A/(1+\exp(B-Kt)) \qquad Y=173.5/(1+\exp(0.156-19.86t))$$

Where Y is the chick weight (g), A is the asymptotic weight, B is the shape constant, K is the growth constant, and t is chick age (days).

The fitted curve accounted for 91.2% of the variance and is plotted graphically in Figure 5.4.

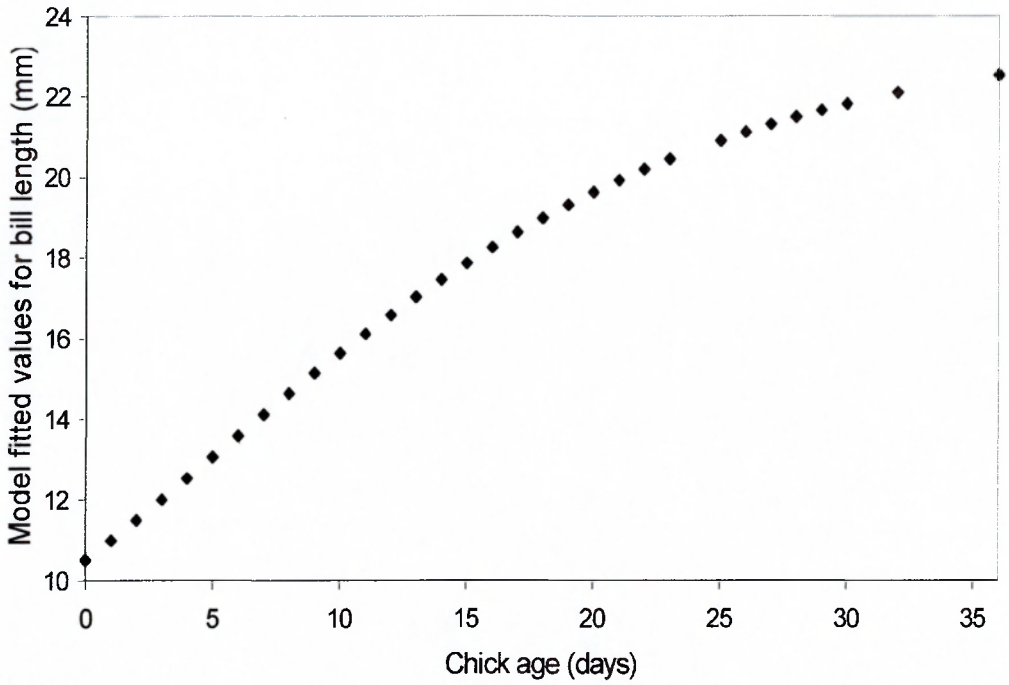

Figure 5.3. Fitted model values for bill length (mm) in relation to chick age (days) as calculated from the growth model of best fit (Gompertz growth curve). See text for parameter estimates.

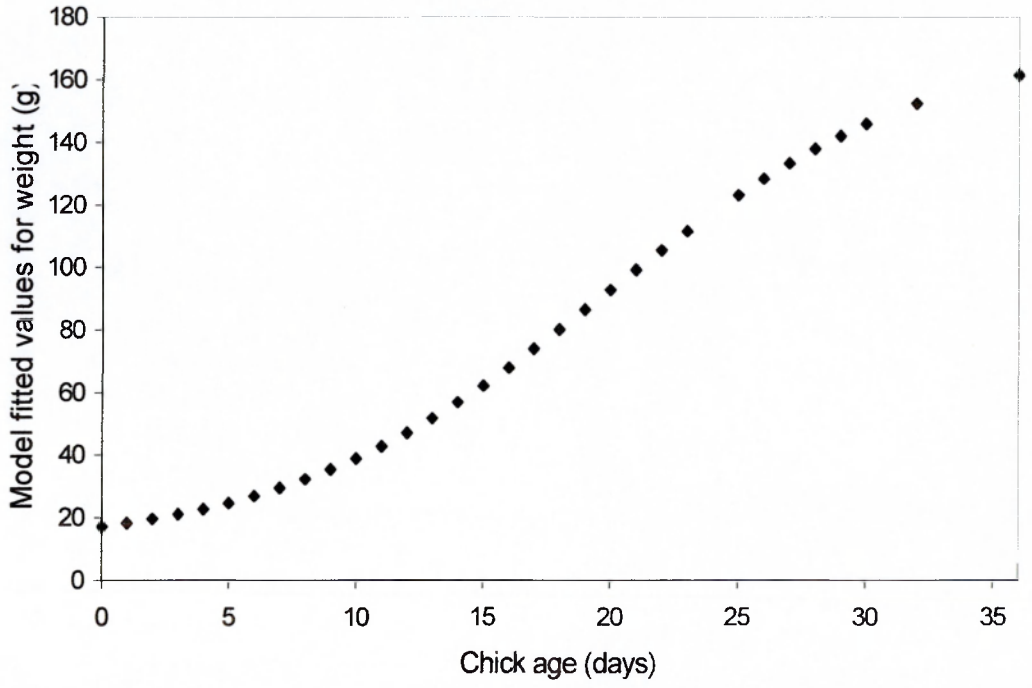

Figure 5.4. Fitted model values for weight (g) in relation to chick age (days) as calculated from the growth model of best fit (logistic growth curve). See text for parameter estimates.

5.3.3 Chick growth rates.

Only data collected from the Shropshire study area is used in the calculation of chick growth rates. A total of 178 mean daily growth rates were calculated for 80 chicks, an average of 2.2 measurements per chick. Daily growth rates ranged from –3.7g/day to 10.6g/day, with an average of 3.04±2.18g/day. The relationship between chick age and daily growth rate suggested a quadratic relationship, with growth rates peaking at around 20 days, thereafter daily growth rates declined, a fitted model gives the equation:

$$y = -0.0148x^2 + 0.5421x + 0.218 \ (r^2=0.45, P=0.007, n=178)$$

However, these data should be treated with caution due to possible pseudo-replication by taking more than one measure per chick.

Mean daily growth rates were estimated per chick (n=80) by summing all growth estimates and dividing by the number of such estimates. Daily growth rates ranged from –1.0g/day to 7.1g/day, with an average of 2.54±1.53g/day. Data were collected from chicks across a variety of crop types. Where chicks were present in more than one crop, the crop type in which they spent most of their intervening time was treated as the crop type. Again data are not strictly independent as chicks from the same brood were not treated separately. However, a visual assessment of mean daily growth rates per chick in relation to crop category (Figure 5.5) suggests that chicks associated with winter crops grew more rapidly than chicks in other crops, but there was little difference between other crop categories.

The mean daily growth rate per brood (n=32) was 2.54±1.36g/day; minimum of –0.1g/day and maximum of 5.7g/day. Broods were treated as being independent of each other and a GLM procedure adopted. Average brood condition was retained in the model (Figure 5.6), but all other explanatory variables, including quadratic and second-order interaction terms, were not significant. There was no effect of crop type on mean brood growth rates but the sample size for some crops were small (Option 1B=5; set-aside=9; spring crops=14; winter crops=2; grass=2). There was no

evidence to suggest that there was any serious degree of spatial autocorrelation within the dataset as a farm term entered into the final model was non-significant.

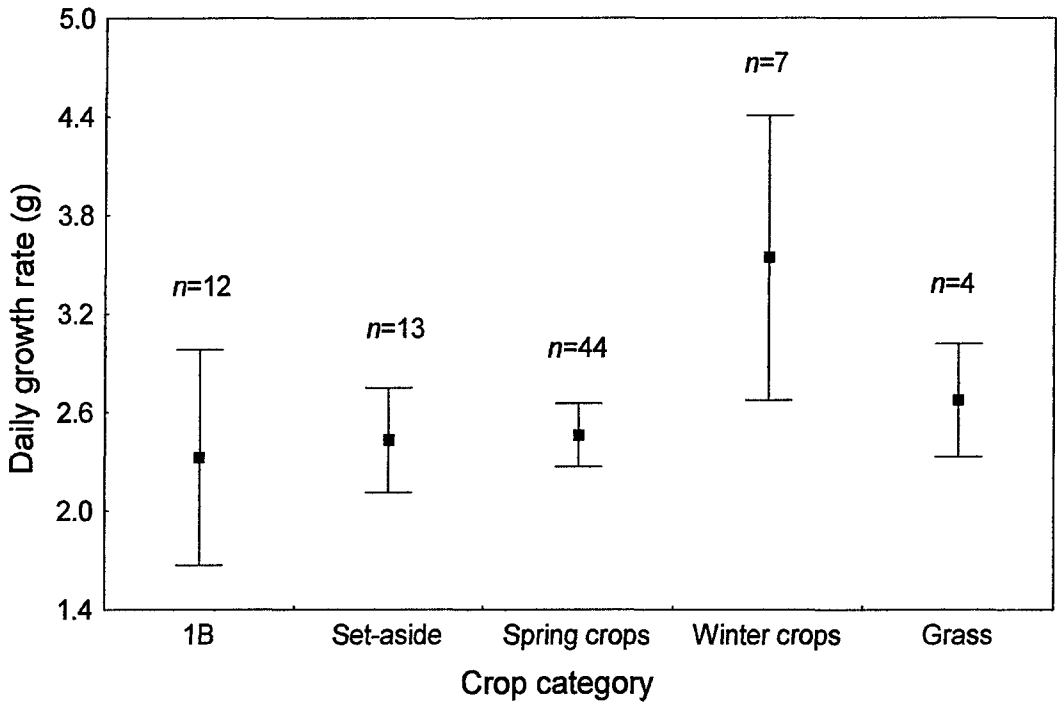

Figure 5.5. Mean growth rate of all chicks associated with different crop types. Means with one standard error are shown. Note, chicks from the same brood were not treated separately.

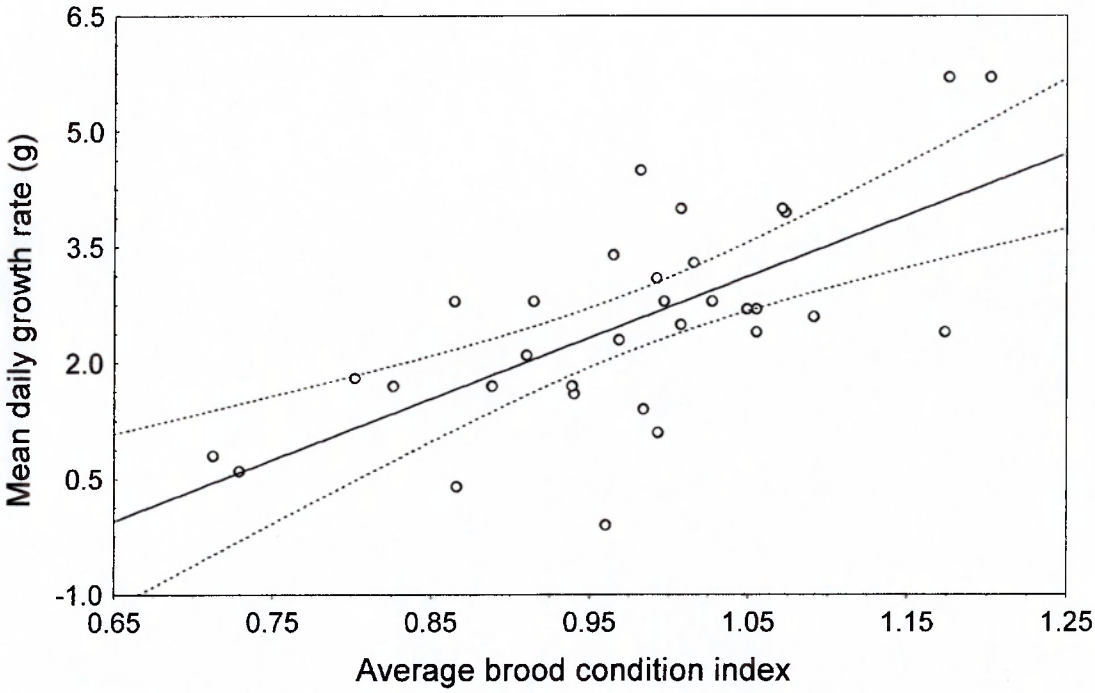

Figure 5.6. Mean brood growth rate (g/day) in relation to mean brood condition index. The solid line represents the fitted regression model, with 95% confidence limits (dashed lines).

5.3.4 Chick condition

Only data collected from the Shropshire study area is used in the calculation of chick condition indices. A total of 145 measurements were used to calculate a model of the relationship between bill length and chick weight (Figure 5.7). Standardised chick weights were then calculated from the model:

$$y=5.769*0.981^{x}$$

The standard weights were calculated by insertion of bill length (y) into the equation to give the related standardised weight (x). Standardised weights from this study, the Cambridge data* (Kirby & Tyler, 1999) and a Dutch study (Beintema, 1994) are given for comparison (Table 5.2).

* The standardised weights using data from the Cambridge study area were reported in Kirby & Tyler (1999). They are replicated here to illustrate that geographically distant Lapwing populations can have subtle differences in standardised weights and thus chick condition indices, although some of this difference is also attributable to a difference in sample size.

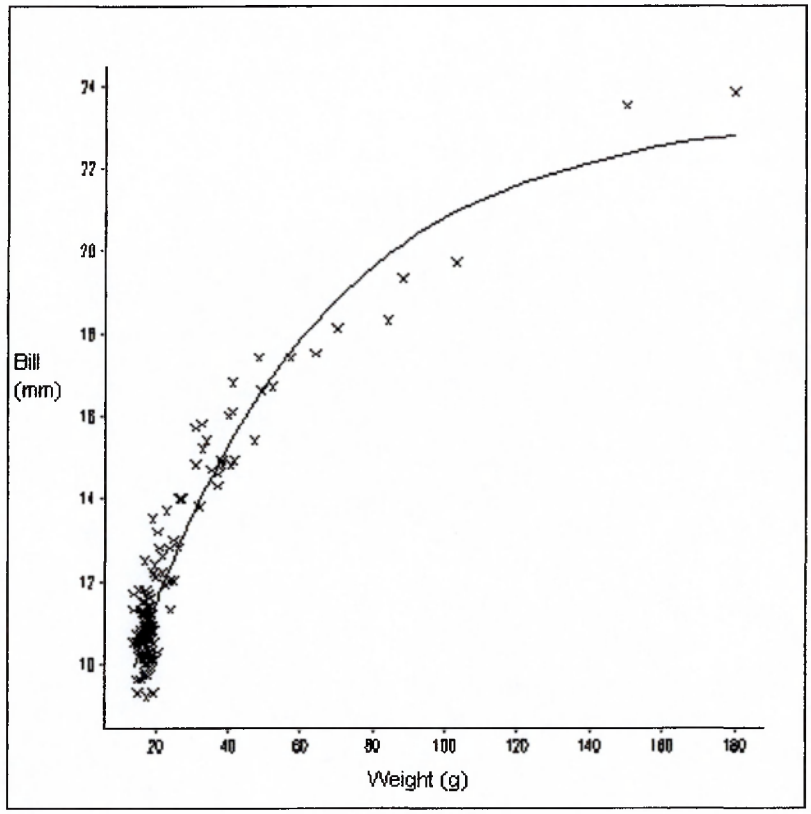

Figure 5.7. Bill length versus weight curve of 145 chick measurements measured at low average SMD (<=20.0mm).

Table 5.2. Standardised weights of Lapwing chicks in Shropshire area, compared to those devised by Beintema (1994) and Kirby & Tyler (1999).

Bill length (mm)	Shropshire standard weight (g)	Cambridge standard weight (g)	Dutch standard weight (g)
10	14	16	16
11	18	17	17
12	22	21	19
13	27	27	21
14	32	32	28
15	38	37	36
16	45	44	45
17	53	52	54
18	62	62	65
19	72	74	80
20	85	92	96
21	104	114	114
22	134	142	128
23	No data	No data	135

Using the standardised weights from Table 5.2, a total of 528 BCI values were calculated for 288 chicks (including chicks of uncertain age), with a mean value of 1.031 (se=0.009, sd=0.198), minimum value of 0.592, and a maximum value of 1.724.

For chicks of a very young age, BCIs were positively influenced by mean egg volume (section 5.3.1), hence chicks <4 days were excluded from further analysis. Chicks of unknown age tended to be older chicks from broods of an unknown origin. This has the potential to introduce bias to the dataset as older chicks are likely to have higher BCIs. A further reduction of the data was done by excluding all chicks of unknown age.

This left a data set of 158 BCIs from 78 chicks of a known age. This data set was used to visually assess the influence of crop categories on chick condition (Figure 5.8). Measurements taken on Option 1B had the highest mean value (1.195), and grass habitats had the lowest mean value (0.923). Only chicks on Option 1B (1.195) and winter cereals (1.009) had values greater than the

average (i.e. >1.0). However, these results should be interpreted with caution as there is the potential for pseudo-replication on two levels, firstly measurements from the same chicks are likely to be similar, and secondly chicks from the same brood are likely to be in similar condition.

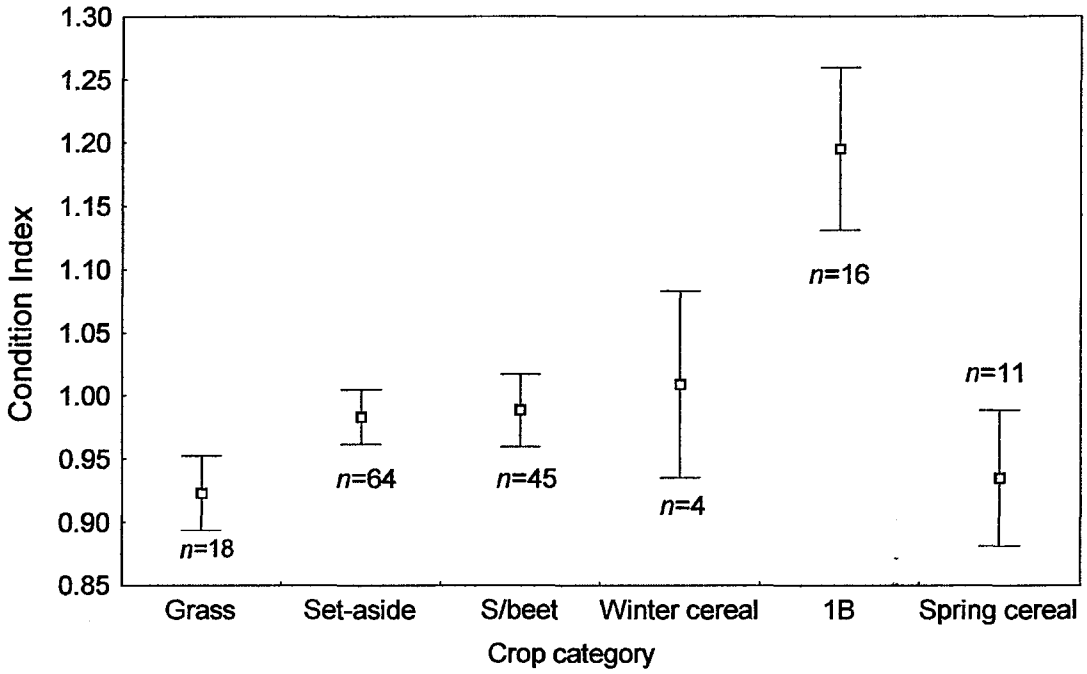

Figure 5.8. Mean Body Condition Index by crop type. More than one BCI per chick is included so there exists the potential for pseudo-replication.

To overcome problems of non-independence of data and pseudo-replication brood average BCIs were calculated for all broods of known age. This left a dataset consisting of BCIs for 32 broods, with a mean value of 0.966±0.024, a minimum value of 0.678, and a maximum value of 1.202. Broods were treated as being independent of each other and a GLM procedure adopted. All explanatory variables and two-way interactions were deleted from the maximal model, as were quadratic effects. A categorical crop type variable was not entered into the modelling procedure due to the small sample size of some crop categories (winter crops and grass). Winter crops appear to have the highest average brood BCI (1.044) but the sample size is small (Figure 5.9). All other groups are similar (average BCIs range from 0.961 to 0.994).

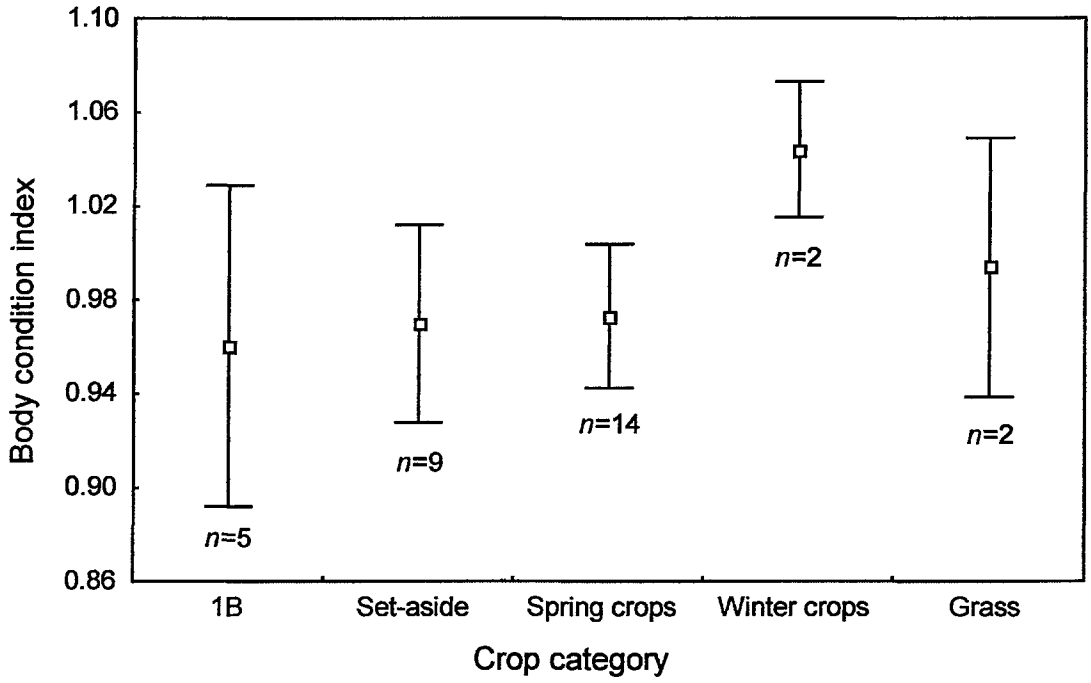

Figure 5.9. Mean brood body condition indices by crop category

5.3.5 Chick survival

5.3.5.1 *Shropshire 1999*

A total of 115 chicks, all from known nests, hatched in the Shropshire study area in 1999. Of these, only 55 were metal-ringed. Errors in the calculation of hatching date meant that most chicks were not ringed in the nest scrape. Chick mortality was thought to be high during the first few days, as many chicks disappeared (or died) yet alarming adults were still present protecting part broods. As it was difficult to determine the exact time of death of individual chicks, an estimate of chick survival to fledging age was calculated by determining the cumulative proportion of chicks that survived from day 1 to day 2, and so on, up to 35 days, ie fledging age (Figure 5.10). Only 11% of all hatched chicks reached fledging age. Data were sufficient to allow a simple comparison of chick survival, using the non-parametric log rank statistic, between those chicks that hatched on Option 1B compared to all other crop types combined. There was no significant difference in the survival rate between the two groups (χ^2=0.55, 1df, P>0.05). Of the chicks that hatched from early nests (see section 3.2.2.3), 11 out of 59 (19%) survived to reach fledging age, compared to 2 out of

56 (4%) that hatched from late nests, although the difference was non-significant (χ^2=3.18, 1df, P>0.05)

5.3.5.2 *Shropshire 2000*

A total of 319 chicks (of known origin) were known to have hatched, of which 14 were known to have reached fledging age. This gives an overall fledging rate of 4%. However, this survival rate based on known hatched chicks only, is likely to be an underestimate for two reasons. Firstly, only 254 of the 319 hatched chicks were ringed (using only the sample of ringed chicks, fledging rate improves to 6%). Secondly, there is a degree of uncertainty in re-locating metal ringed chicks due to difficulties in observing chicks in taller vegetation or in finding chicks if they make movements away from the natal field.

Of the 88 chicks that hatched from replacement nests (after 23rd April) none were known to have fledged.

A total of 51 chicks were fitted with radio transmitters for a total of 595 tag days. Eight radio-tagged chicks were known to have fledged. A GLM procedure was adopted and all explanatory variables were deleted from the null model. The null model gives a daily survival rate of 0.9378 that results in a fledging rate (assuming 35 days to fledging) of 10.6% (Figure 5.11). However, some chicks in the Cambridge study area were known to fledge at 30 days. If survival is calculated to 30 days then the fledging rate improves to 14.5%.

Of the 51 tagged chicks, 8 fledged, 19 were recovered with evidence of predation, and the outcome for 24 tags was unknown (evidence from the Ouse Washes suggests that tags that are not relocated tend to be predated, G. Tyler *pers. comm.*),

Despite the lack of significance of chick condition on survival, there was a significant difference in mean BCI between chicks that were known to be predated (n=9, mean=0.941; median=0.962), and known to have fledged (n=7, mean=1.102; median=1.122) (Mann Whitney U=9.0, P=0.017; Figure 5.12).

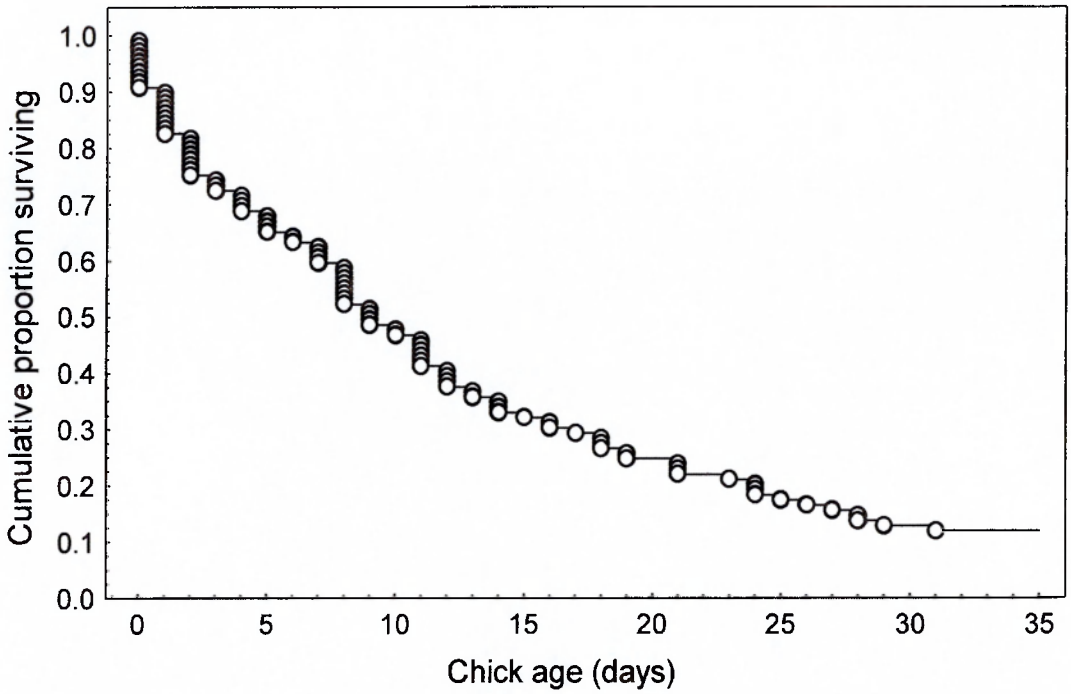

Figure 5.10. The cumulative proportion of chicks surviving to fledging age (35 days) in the Shropshire study area in 1999.

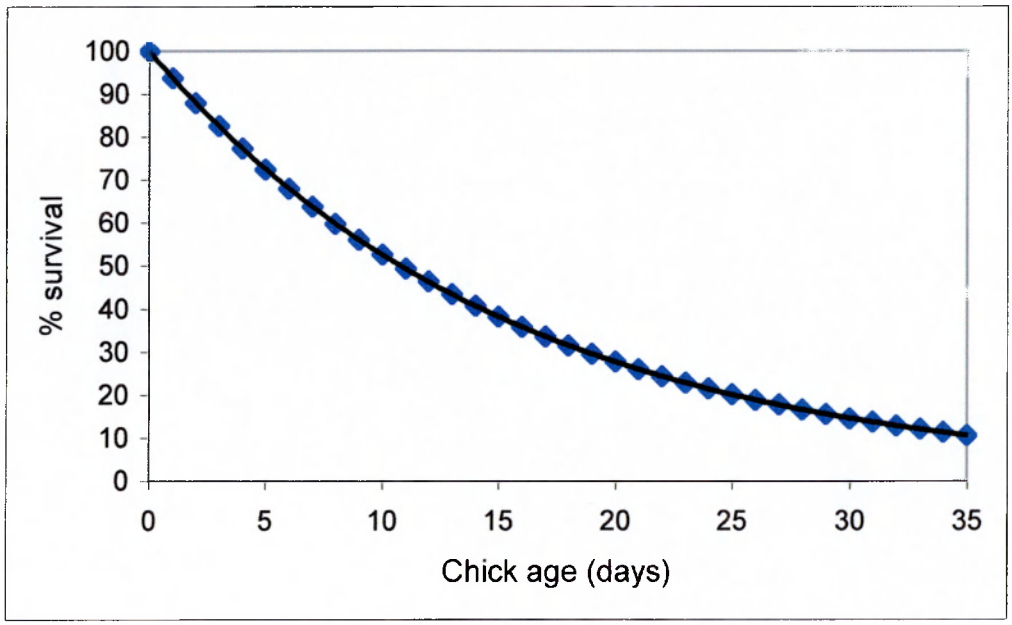

Figure 5.11. Chick survival for radio tagged chicks in Shropshire 2000. Resulting a fledging rate of 10.6% or 14.5% if fledging age is calculated to 35 or 30 days respectively.

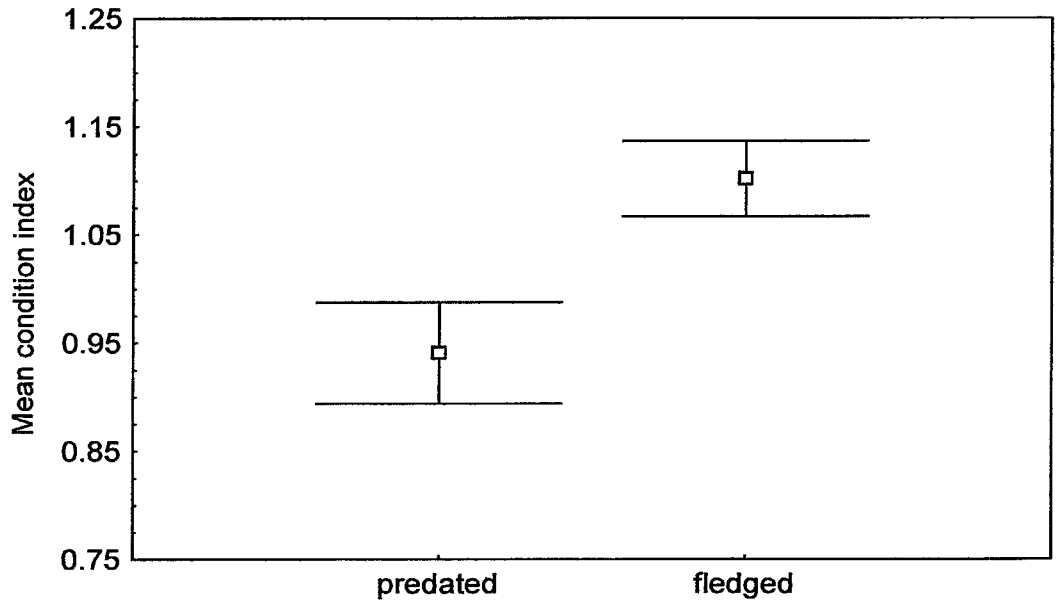

Figure 5.12. Mean body condition of radio tagged chicks that were predated (n=9) or fledged (n=7).

Table 5.3. Measures of chick survival and chick productivity estimates for 1999 and 2000 data (chicks of known origin only). The Cambridge data is incorporated here for comparison.

	Chicks hatched	Chicks fledged	Chick survival	Fledgings per nest	Fledgings per brood	Minimum chick productivity per female per year	Maximum chick productivity per female per year
Shropshire 1999						0.23	0.43
Total	115	13	0.11	0.23 (56)	0.39 (33)		
Option 1B	58	9	0.16	0.47 (19)	0.56 (16)		
Other crop types	57	4	0.07	0.11 (37)	0.24 (17)		
Early nests	59	11	0.19	0.37 (30)	0.61 (18)		
Relay nests	56	2	0.04	0.08 (26)	0.13 (15)		
Shropshire 2000						0.11	0.15
Total	319	14	0.04	0.11 (132)	0.15 (94)		
Option 1B	48	3	0.06	0.2 (15)	0.23 (13)		
Other crop types	271	11	0.04	0.09 (117)	0.14 (81)		
Early nests	231	14	0.06	0.15 (95)	0.21 (68)		
Relay nests	88	0	0	0 (33)	0 (28)		
Cambridge 1999						0.16	0.21
Total	149	8	0.05	0.16 (49)	0.20 (41)		
Early nests	106	3	0.02	0.08 (38)	0.10 (31)		
Relay nests	43	5	0.12	0.45 (11)	0.50 (10)		

5.3.6 Chick productivity estimates

Minimum and maximum estimates of chick productivity varied from 0.11 (Shropshire 2000) to 0.43 (Shropshire 1999) (Table 5.3). This rather simplistic approach to calculating productivity makes no attempt to incorporate other demographic parameters of importance, such as mean clutch size and nest survival.

Table 5.4 incorporates a mean clutch size of 3.81 (Chapter 2) and crop specific nest survival rates (Chapter 4) in a calculation of crop specific breeding productivity. Overall chick productivity was 0.28 chicks per female per year, with females that nested on Option 1B producing the most young (0.32) and grass habitats producing the least young (0.1).

Table 5.4 Chick productivity estimates derived from demographic parameters quantified elsewhere in this thesis.

	Mean clutch size	Nest survival	Chick survival	Productivity[1,2,3]
Overall	3.81	0.68	0.11	**0.37** *0.28* (0.09)
Winter crops	3.81	0.55	0.11	**0.33** *0.23* (0.10)
Spring cereal	3.81	0.27	0.11	**0.18** *0.11* (0.07)
Spring crops	3.81	0.61	0.11	**0.36** *0.26* (0.10)
Set-aside	3.81	0.47	0.11	**0.31** *0.20* (0.11)
Option 1B	3.81	0.76	0.11	**0.40** *0.32* (0.08)
Stubbles	3.81	0.28	0.11	**0.21** *0.12* (0.09)
Grass	3.81	0.23	0.11	**0.18** *0.10* (0.08)

[1] Figures in bold give the overall productivity per female per year.

[2] Figures in italics give the productivity estimates for the first nesting attempt.

[3] Figures in parentheses give the productivity estimates for the re-nesting attempts.

5.3.7 Habitat use and movements of foraging chicks

In both years in the Shropshire study area, chicks were located in a broad range of crop types throughout the breeding season. There was a general trend of fewer crops being utilised as the breeding season progressed, suggesting that some crops became unsuitable for chick-rearing. Data from 1999 shows that at the start of the chick-rearing period chicks were mainly associated with set-aside (Figure 5.13). During early to mid May chicks were found in a wide variety of crop types, but by mid June Option 1B fields were the main chick-rearing habitat. In 2000, brood use at the end of the breeding season was confined to sugar beet, set-aside, grassland and Option 1B (Figure 5.14). In both years, winter crops were utilised by chicks/broods in small amounts at the start of the chick-rearing period, despite winter cereals accounting for about 50% of the study area. Furthermore, very little use was made of pasture and grass habitats, particularly in 1999.

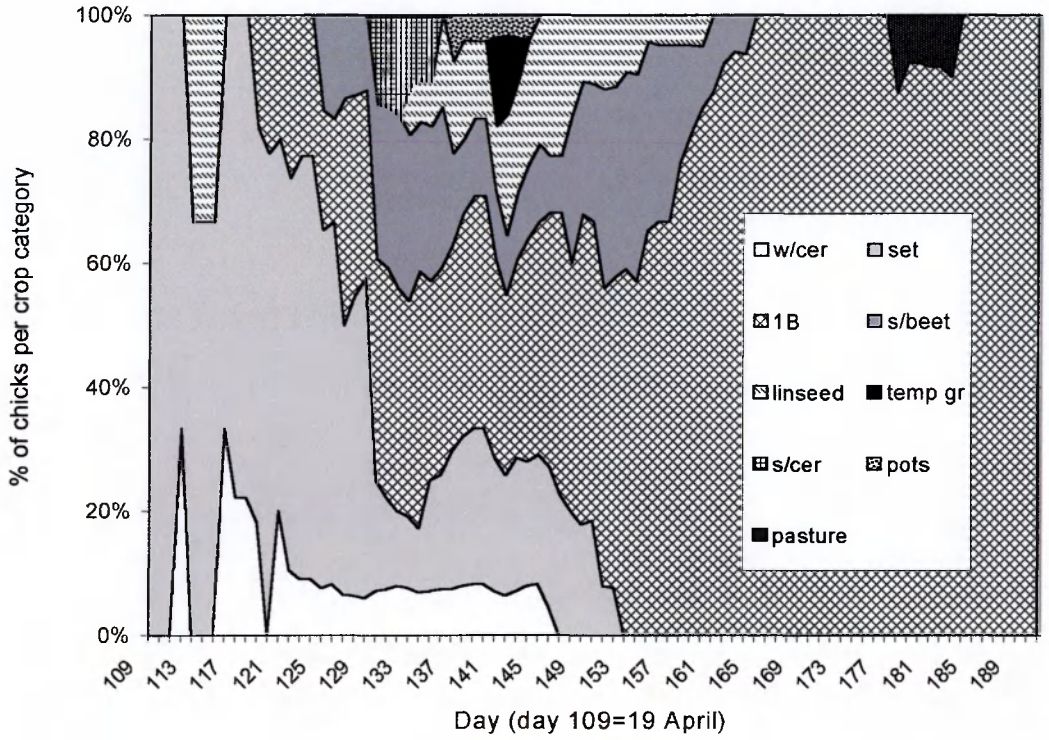

Figure 5.13. Temporal patterns in crop use by Lapwing chicks during the1999 breeding season

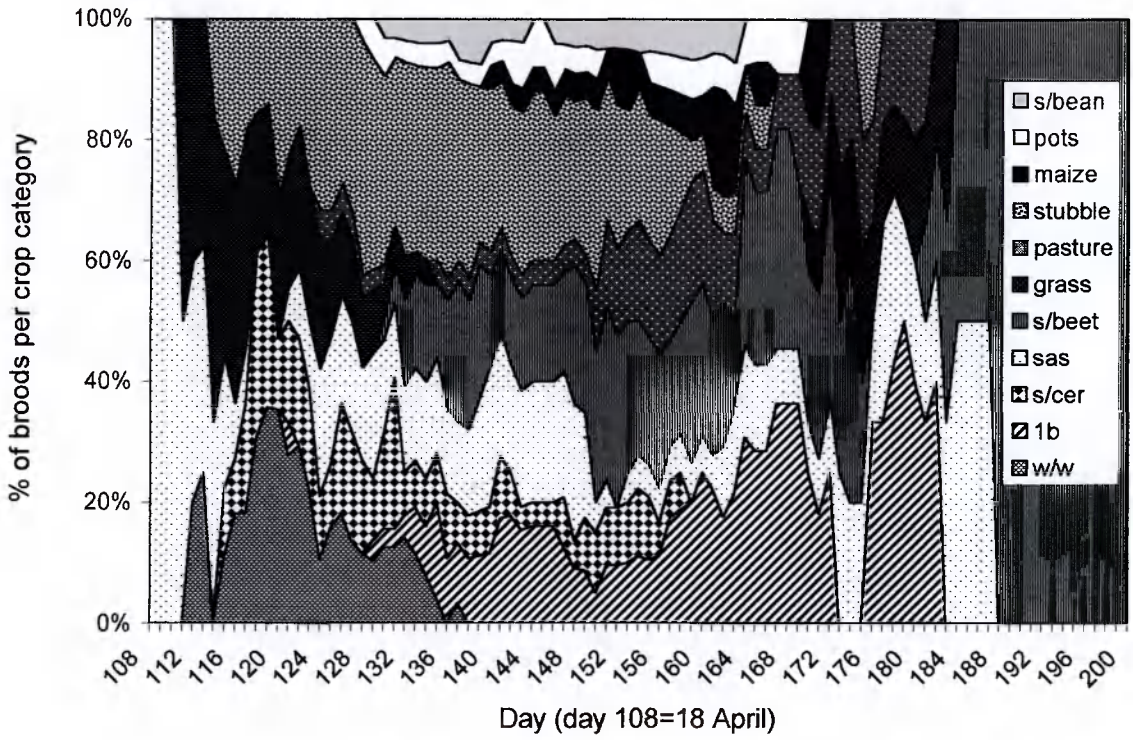

Figure 5.14. Temporal patterns in crop use by Lapwing broods during the 2000 field season.

5.3.8 Chick movements

5.3.8.1 *Shropshire 1999*

Of the 33 broods only one was relocated outside the natal field. The brood dispersed from permanent set-aside grass and was subsequently relocated in spring-sown triticale and finally in spring-sown linseed. A large number of broods were associated with Option 1B and set-aside which may explain the lack of dispersal in this cohort (see 2000 data)

5.3.8.2 *Cambridge 1999*

Data were collected from 40 broods, of which 26 (65%) were relocated away from their natal field. The mean distance moved by broods was 853.9m (s.e.=182.5), with a total brood movement of 34157m. The cumulative distance moved between fields by one brood was 4225m (Figure 5.15).

Of the 40 broods only 9 produced fledged chicks. Broods that contained chicks that eventually fledged, travelled further (mean and median distances of 1592m and 640m respectively) than broods with no fledged young (mean and median distances of 850m and 450m respectively). Although, the difference between the two groups was non-significant (Mann Whitney U=99.0, P=0.19).

5.3.8.3 *Shropshire 2000*

Data were collected from 62 broods of which 20 (32%) moved out of their natal field. The mean distance moved by broods was 156m (s.e.=42.5), with a total brood movement of 9675m. Most movements were small usually to adjacent fields, the greatest distance covered by any single brood was 1775m (Figure 5.15).

Of the 62 broods only 14 produced chicks that went on to fledge. Broods that produced fledged chicks moved greater distances (mean and median distances of 308.9m and 162.5m respectively) than those that failed to produce fledged young (mean and median distances of 116.7m and 0m respectively) (Mann Whitney U=209.5, P=0.033).

In Shropshire 1999, the majority of broods were associated with set-aside and Option 1B and movement out of natal fields were limited. However a comparison of brood movements between the Cambridge 1999 cohort and the Shropshire 2000 cohort shows that broods in the Cambridge area moved significantly greater distances than those in the Shropshire area (Mann Whitney U=695.5, P=<0.001; Figure 5.15)

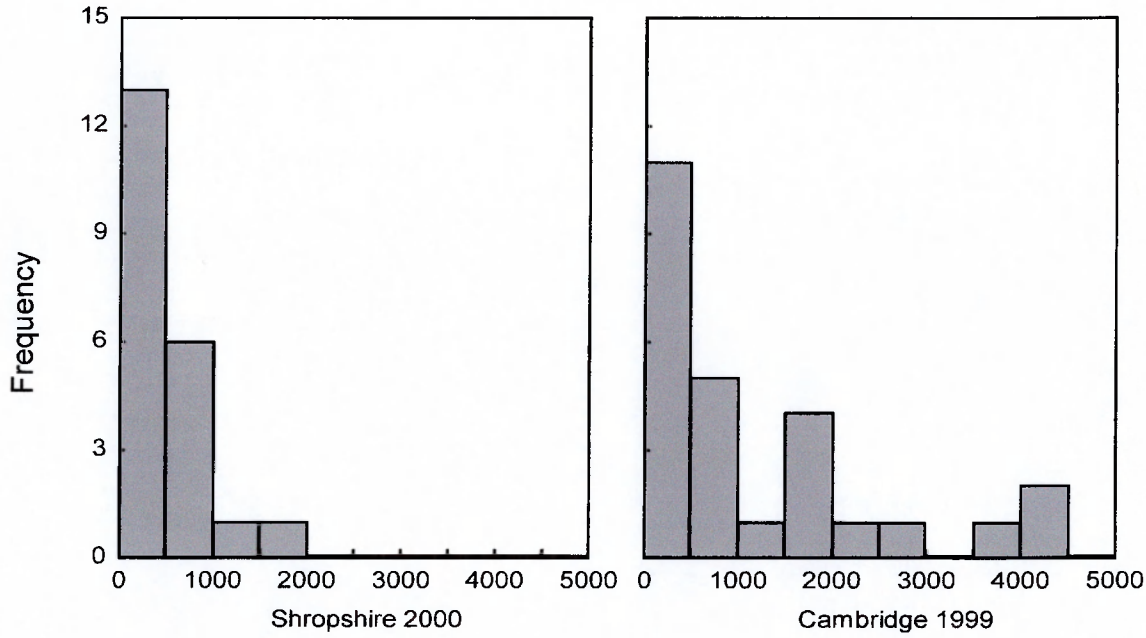

Figure 5.15. Comparison of distances moved by chicks in the Cambridge and Shropshire study areas. Each distance to category is 500m. Note the lack of movements greater than 2000m in Shropshire.

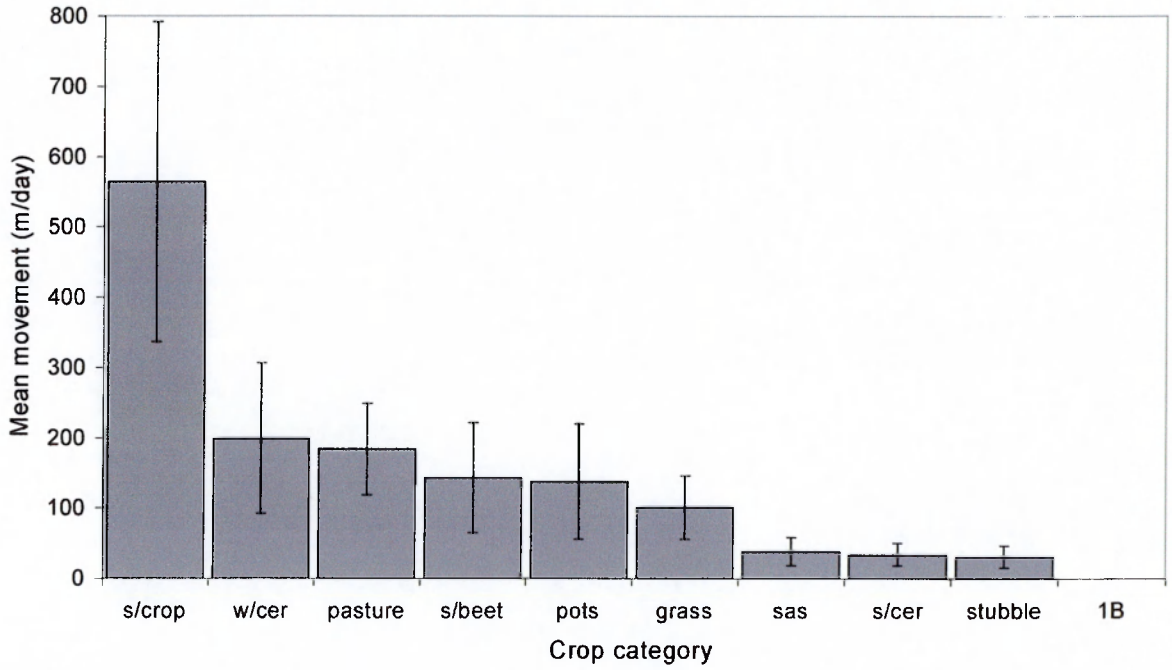

Figure 5.16. Mean rate of movement (m/day) out of different crop types, for Cambridge & Shropshire data (radio tagged chicks only). One standard error is shown.

Rates of movement from crop types differed between crop categories, Kruskal $Wallis_{9,243}=28.46$, $P=<0.001$ (Figure 5.16), with the most rapid movements from spring crops (linseed, beans and peas), although the small sample size ($n=5$) suggests this result should be interpreted with caution. If data from spring crops are excluded from the analysis the difference is still significant but the significance is reduced ($KW_{8,238}=16.3$, $P=0.04$). If Option 1B data are excluded from the analysis the differences between crop types are no longer significant ($KW_{7,227}=13.5$, $P=0.06$). As the data are highly skewed median and modal averages for average daily movements are zero for all crop categories, hence for illustrative purposes the mean daily movements between crops are plotted to visually assess inter-crop differences (Figure 5.16). Movements from spring crops (565m/day) and winter cereal (199m/day) are the most rapid and stubbles (31m/day), spring cereals (34m/day) and set-aside (38m/day) the least rapid. Radio tagged chicks on Option 1B fields were never known to disperse from these fields.

Daily rates of movement, irrespective of crop type, were significantly different between the two study areas (Mann Whitney U=5209, $P=0.013$). These data were also highly skewed with both regions having median averages of 0m. Mean daily rates of movement were 9m (range=0-175m) and 115m (range=0-1345m) for Shropshire and Cambridge respectively.

The data used in Figures 5.14 & 5.16 are summarised in Table 5.5 to show the relative importance of the different measures of habitat use by Lapwing broods. Set-aside is the crop that is used the latest and for the highest number of days. Winter cereal and grass silage fields were not used past mid May and only for a period of about 3 weeks; most chicks which hatched in these fields were moved soon after hatching.

Table 5.5. An assessment of the suitability of crop types using 3 different measures of habitat use. For each column the figures in parentheses are the ranking for that particular measurement, an average ranking for all 3 measurements is given for each crop type.

Crop type	Last day recorded[1]	Number of days used[1]	Mean daily movement (m)[2]	Average rank
Set-aside	205 (1)	97; range=108-205; (1)	38 (3)	1.7
Option 1B	182 (4)	61; range=121-182; (4)	0 (1)	3
Grass (min)[3]	183 (3)	72; range=111-183; (2)	101 (4)	3
Sugar beet	201 (2)	71; range=130-201; (3)	143 (7)	4
Spring cereal	158 (9)	43; range=115-158; (6)	34 (2)	5.7
Pasture	181 (5)	57; range=124-181; (5)	184 (8)	6
Potatoes	169 (7)	41; range=128-169; (7)	138 (6)	6.7
Maize	171 (6)	31; range=140-171; (9)	564 (10)	8.3
Beans	163 (8)	33; range=130-163; (8)	564 (10)	8.7
Grass (max)[3]	134 (11)	23; range=111-134; (11)	101 (4)	8.7
Winter cereal	137 (10)	25; range=112-137; (10)	199 (9)	9.7

[1] days are recorded as the number of days since 1st January

[2] mean daily movements are taken from Figure 5.14

[3] the nature of the grass fields was very variable and have been separated here for comparison, although the sample size is small. Grass (min) refers to fields generally with shorter and less dense grass, such as grass leys and set-aside sown with a grass mix. Grass (max) were characterised with tall, dense swards cut for silage.

5.4 DISCUSSION

5.4.1 Egg volume and chick weight at hatching

As has been shown in other studies, Lapwing chick weight at hatching is positively correlated with egg volume (Galbraith 1988b; Hegyi, 1996; Blomqvist *et al*, 1997; Linsley 1999). Large Lapwing eggs have greater yolk, lipid and energy contents, and consequently produce heavier chicks which probably have larger yolk and protein reserves which enables chicks to counter adverse extrinsic factors during the first few days post-hatching. Parsons (1970) suggested that large eggs produced more viable chicks in the semi-precocial Herring Gull *Larus argentatus* because they hatched with larger yolk reserves, and thus the larger energy stores increased chick survival during the first few days. This effect was not apparent in this study as the mean egg volume was non-significant in the modelling procedure when investigating chick survival. The lack of an effect of egg volume on chick survival is likely for two reasons. Firstly, environmental conditions were not the limiting factor in this population. Food resources could have been sufficient to enable chicks to meet daily energy requirements, which reduces the need to undertake hazardous post hatching movements. Alternatively, if predation was the major cause of chick mortality in the first few days after hatching, then large egg size would not manifest itself through enhanced chick survival; although this assumes that the chance of a chick being predated is the same for all chicks.

The relationship between bill length and body weight has been suggested to be a better determinant of 'fitness' than a measure of chick weight on its own. This is the first time that chick condition at hatching has been shown to be correlated to mean egg volume in the Lapwing.

5.4.2 Growth patterns and growth rate

The general pattern of chick growth in Lapwings has been well documented and all studies have shown the general pattern to be similar, that is, little change in weight in the first few days followed by a period of accelerating growth and a final plateauing out as the chicks reach fledging age. This would suggest that the general pattern of growth of Lapwing chicks is adaptive and largely genetically determined (as suggested by Galbraith 1988d). However, a number of extrinsic

factors may contribute to subtle differences between years and between geographically distant populations:

i) egg volume and chick size at hatching,

ii) habitat effects (on food availability and the subsequent need to move between fields),

iii) seasonality (mainly through changes in weather),

iv) predation pressure.

Galbraith (1988d) suggests that in the first few days chicks may have little time for feeding and must rely on yolk reserves, as the priority is to move to chick-rearing areas. Galbraith (1988d) and Redfern (1983) both show that chicks initially lost weight and delayed growth in the first few days, probably due to intense brooding to meet thermo-regulatory requirements. However, this was not apparent from this data as chicks generally gained weight in the first few days post-hatching. Similarly, Jackson & Jackson (1975) found that chicks gained weight post-hatching, and suggested differences in growth characteristics between populations may be explained by regional differences in the environmental conditions listed above. Captive reared Lapwing chicks do not exhibit this early weight loss, probably due to the lack of exposure to adverse environmental conditions (Beintema & Visser, 1989a)

The growth rate constant K (0.086) as determined by the Gompertz growth curve (Figure 5.3) is similar to that given by Redfern (1983) of 0.079 for Lapwings, and is largely comparable to growth rates of other precocial wader species (Ricklefs, 1967). The growth rate of chicks was shown to be positively affected by chick condition. Those chicks that were in good condition grew faster. Chicks that are in good condition are likely to require less brooding by adults and can spend more time foraging and consequently grow faster.

There was no difference in growth rates between crop types suggesting that food resources were sufficient to meet daily energy requirements. Bak & Ettrup (1985) found that chicks gained weight slowly during the first week of life and during the final days prior to fledging (2.5 and 2.0g/day, respectively) more rapidly from the second week through the fifth week (4.9 g/day). The daily weight gain was greatest in salt marshes and least in arable, probably reflecting differences in food

supplies. Mean daily growth rates of broods in this study (2.54g/day) are low compared to growth estimates derived from upland grass habitats. Baines (1990) estimates growth rates of 5.7g per day in areas of high food availability and 5.3g per day in fields of low food availability and argued that food was not a limiting factor in his study population. Only in one year out of three was chick daily weight gain significantly different on unimproved pastures when compared to improved pastures, and this particular year was characterised by low rainfall, and was explained by an effect on reducing soil invertebrate activity near the soil surface. A cold year reduced growth rates on both improved and unimproved pasture when compared to the other two years, highlighting the impact of weather on chick growth rates. Similarly, in The Netherlands, Beintema *et al.,* (1991) found that weight gain decreased in dry springs for Lapwing chicks, and suggested that this was due to effects on food availability, particularly energy-rich earthworms which are less active near the soil surface in dry soil conditions. Furthermore, chicks show retarded growth from mid May onwards and Beintema *et al.* (1991) suggest this was due to prey profitability. However, in the Shropshire study area, a date variable was deleted from the modelling procedure of growth rates, which would suggest that there was no temporal effect on growth rate of Lapwing chicks in this study (it should be noted that in both years soil moisture deficit was never very high for extended periods of time).

A greater understanding is required of the subtle interactions between weather conditions, food availability, sward structure and chick growth/condition. Indeed, these interactions may be of increasing relevance given the future projections of rapid climate change, and the resulting shifts in weather patterns. These need to be investigated in terms of micro-climatic features such as ground temperature, soil moisture and chill effects caused by damp vegetation. Tall, dense vegetation is cool and moist, compared to lower, more open vegetation (Beintema & Visser, 1989a).

5.4.3 Chick condition

In this study chick condition did not appear to be effected by any of the measured variables. There was some indication that broods on winter crops were in better condition than on other crop types,

but sample sizes were small. Taking individual chicks as the unit of analysis suggests that the mean body condition index was highest in chicks on Option 1B (Figure 5.8), but data are not independent, and must be interpreted with caution. However, as chicks rarely moved out of Option 1B fields (suggesting adequate food resources), this interpretation does seem valid.

Previous analyses of the Cambridge dataset (Kirby & Tyler, 1999) had shown that chick condition was negatively associated with soil moisture deficit. This was not apparent in Shropshire, probably due to few periods of prolonged dry weather associated with 2000. In some years soil moisture is likely to be a crucial factor influencing chick condition, due to the effect on earthworms, which are an energy rich source of food for chicks. Chicks have been shown to favour damp areas for foraging in a variety of habitat types; arable (chapter 6); grassland (Milsom et al., 2000); and upland (O'Brien, 2000).

Although chick condition was shown to have a non-significant effect on chick survival, there was some evidence to suggest that condition can exert an influence on the likelihood of predation (Figure 5.10). Personal observations suggested that chicks that were in poor condition were often foraging in sub-optimal habitat, such as gate entrances and adjacent to hedgerows, where they may be more susceptible to predation. However, more work is required to determine the interactions between chick condition, foraging behaviour and predation.

5.4.4 Chick survival

Chick survival was poor in both years, the most accurate assessment using radio tracking data suggests less than 11% of chicks reach fledging age. None of the measured variables were found to significantly affect survival rates, and most interestingly survival rates did not differ between crop types. Chick age had a non-significant effect on survival rates, which suggests that in this population mortality occurred throughout the pre-fledging period. Many studies have shown that mortality is most severe during the first few days post-hatching, yet this was less apparent in this study. This could be explained by the lack of movements by broods in the Shropshire area, where average movements were generally short. On arable land in Lancashire, Linsley (1999) reported enhanced chick survival when arable nest-sites were in close proximity to pasture (overall chick

survival was 14.7%). Similarly, Galbraith (1998a) showed that chicks with access to suitable pasture fields undertook shorter movements and survived better than chicks that hatched without easy access to pasture. Linsley (1999) found that in years where chicks remained in their natal fields chick survival was increased, primarily as a result of fewer mortality incidents of drowning in steep-sided ditches when moving between fields. However losses due to movements were not confined to young chicks as in one year fledging success was associated with a higher level of mortality of chicks over ten days old due to delayed movement from natal fields.

Galbraith (1998a) gives an overall fledging success of 25%, with differences in fledging success between chicks on arable land and rough grazing. Chicks on arable land suffered high post-hatching mortality where c. 80% of chicks less than 10 days old died, compared with only 50% on the rough grazing site. French *et al.* (2000) give an overall chick survival estimate of 13%, varying from 0 to 38% in 8 study sites along a 10 km stretch of the River Spey valley in Scotland. Of the 8 study sites only one was classed as a mixed arable area, and the chick survival of 15% was low.

Baines (1990) estimated chick survival rates of between 18-29% on arable land compared to 15% on improved grassland and 43% on unimproved pasture. He suggested that the presence of breeding birds on arable land and improved grassland was due to recruitment from unimproved grass. Recent fledging estimates on coastal grazing marshes in England, of only 4%, highlighted cold weather affecting chicks less than 10 days old and predation to be the main causes of mortality (Hart *et al.*, 2002).

In summary, the low chick survival of 11% is not unusual when compared to other recent studies of Lapwing breeding success. However, the inability to collect data during the 2001 Foot and Mouth outbreak prevented an investigation of the main causes of mortality. A high proportion of recovered radio tags (19 out of 51) showed evidence of predation, although it is possible that the chicks could have died of other causes prior to being scavenged. A further 24 out of 51 tags were not relocated, and previous work suggests that a large proportion of these birds would have been predated (Tyler, *pers. comm.*). A rather obvious conclusion would suggest that predation is a significant cause of chick mortality in this study. However, circumstantial evidence of poor chick condition increasing susceptibility to predation requires further investigation.

5.4.5 Chick productivity

Numerous studies have concluded that the driving factor behind the current population decline is linked to changes in the breeding season (Wilson *et al.,* 2001; Catchpole *et al.,* 1999; Hudson *et al.,* 1994; Peach *et al.,* 1994), and increasingly it is believed that a reduction in chick survival is the proximate cause for the current downward population trend. Analysis of ring recovery data (Catchpole *et al.* 1999) has shown that 0.72-0.84 fledged young need to be produced per female per year if a population is to remain stable. Productivity estimates from a variety of studies are given in Chapter 1 (Table 1.7), and show that only 9 out of 23 studies attain the required level of productivity. The overall productivity estimate in this study of 0.37 is about half that required for the population to be self-sustaining. Incorporating clutch size, nest and chick survival estimates into an overall measure of productivity highlights some subtle differences between crop types, with Option 1B (0.4) having the highest overall productivity, and grass and spring cereal fields having the lowest productivity (0.18). These differences between crop types are driven by differences in nest survival. Crop specific differences in chick survival were not detected despite a relatively large sample size (51 radio tagged chicks for a total of 595 tag days). In terms of chick survival, crop type *per se* may not be the most important factor, but the vegetation structure and the food availability within the crop, may be a greater determinant of chick survival. Neither of these variables were measured in sufficient detail in 2000 to allow a quantitative effect on chick survival rates.

5.4.6 Habitat use and chick movements

In this study the variety of crop types used for chick foraging declined as the season progressed, and at the end of the breeding season crop use was confined to Option 1B in 1999 and sugar beet in 2000. Similarly in Cambridge just 3 crop types, permanent pasture, rotational set-aside and sugar beet were used from mid June onwards in 1999. The switch from spring to autumn cropping, decline in mixed farming enterprises, the improved crop varieties and increased fertiliser use which promotes uniform crop structure are likely to have reduced the amount of habitat which is

suitable for chick rearing. The increasing selection for spring cereal fields adjacent to pasture for nest-sites (Wilson *et al.,* 2001) would suggest that more fields are becoming less suitable as nesting sites because they are too distant from preferred chick rearing habitat. However, despite previous work suggesting the importance of grass habitats for chick foraging, this was less evident in this study. In 1999 and 2000 grass habitats were rarely used, and then only by a small percentage of broods (Figures 5.11; 5.12). Indeed in many instances, particularly in relation to Option 1B, 'good quality' cattle grazed pasture was adjacent to nesting fields, but chicks remained on natal fields rather than make short movements to pasture. In many instances, Option 1B was characterised by short, sparse vegetation with lots of bare ground, and it may be that foraging opportunities and food availability was sufficient to negate the need for movements between fields. There was some evidence that chicks on 1B were in good enough condition to justify staying in natal fields. Earthworm abundance was generally lower on 1B than pasture (Chapter 6), but differences in the abundance of surface invertebrates between the two habitat types was not investigated. However, due to the open nature of the sward and the amount of bare soil patches within 1B it is likely that surface invertebrates and earthworms are more visible and thus more available to foraging Lapwings, but this was not investigated. Linsley (1999) showed that rotational set-aside was not used as a brood rearing habitat and concluded that this was due to the nature of the vegetation reducing the foraging efficiency of chicks.

The Cambridge study area was characterised by less diverse cropping in comparison to the Shropshire area, and this is the likely explanation for differences in chick movement distances, with broods in Cambridge having to move larger distances to find suitable foraging areas. The cumulative distance moved between fields of one brood was 4225m, which is the largest distance recorded in the literature. One brood of Cambridgeshire chicks was relocated more than 1500m away from its natal field just 2 days after hatching. Blomqvist & Johansson (1995) showed that distances between nests and chick foraging areas varied between 9 and 332m; brood survival was negatively correlated with the distance moved in 2 years out of 3. Brood movements were significantly longer for broods hatched on arable fields (215 ± 38m) than those hatched on pastures (65 ± 13m). Blomqvist & Johansson (1995) propose that there is a trade-off between nesting on

arable land, where there is the potential to produce large eggs due to the increased availability of large prey items, such as earthworms, and the need to make chicks undertake energetically costly movements between natal and chick rearing habitat.

Broods that produced fledged young moved greater distances than broods that failed to produced fledglings. This suggests that adult Lapwings face an interesting dilemma of whether to force chicks to move large distances, which may increase the susceptibility to predation or starvation risk, or to remain in natal fields that may be devoid of sufficient food or suitable habitat, and starve.

The key findings from this chapter are

i) Chick condition at hatching was shown to be positively correlated with mean egg volume.

ii) Chicks that were known to have fledged were in better condition than those that were known to have been predated.

iii) Chick survival was lower than that required to maintain population stability, and poor survival is likely to be driving the current population decline.

iv) Chicks that hatched on Option 1B fields remained in their natal fields until fledging. Conversely, broods that produced fledged young generally moved greater distances than those broods that failed to produce fledglings.

CHAPTER 6

LAPWING CHICK DIET AND EARTHWORMS

6.1 INTRODUCTION.

Knowledge of Lapwing diet is vital in assessing the quality of different agricultural crop types as sources of food, and to develop agricultural practices that have beneficial effects on Lapwing food resources and ultimately Lapwing breeding success. Lapwings are known to have an eclectic diet with a wide range of taxonomic groups taken; a variety of insects including beetles, flies, mayflies, crickets, grasshoppers and earwigs, as well as other groups such as earthworms, spiders and molluscs have been recorded (see Table 1.4), (Cramp & Simmons, 1983; Wilson *et al.*, 1996).

A major determinant of any species' distribution and reproductive performance within a given landscape must be the way it can utilise it's preferred resources. Earthworms are known to be a major component of Lapwing diet, both for adults (Klomp, 1954; Baines, 1990; Berg, 1993; Blomqvist & Johansson, 1995) and chicks (Galbraith, 1989b; Beintema *et al.,* 1991). The high-energy requirements prior to breeding, for both males (territory defence and courtship) and females (energy reserves for egg formation and incubation), are compensated for by selecting feeding habitats high in prey availability (Galbraith, 1989; Baines, 1990). Blomqvist & Johansson (1995) showed that females foraged mostly on arable fields where the intake rate of earthworms was high. Högstedt (1974) also showed the importance of earthworms in the diet during the pre-breeding season, and furthermore, that the length of the pre-laying period highly correlated with the abundance of lumbricids. In central Sweden Lapwings selected territories with a high proportion of foraging habitats (Berg, 1993).

Galbraith (1989b) showed that chicks take a wide variety of prey items but that the diet was dominated, in terms of occurrence, by earthworms, Tipulid larvae and Coleoptera, and suggested that the chicks were feeding opportunistically rather than selectively. Similarly, Matter (1982) showed from analysis of 39 stomach contents that Coleoptera and Diptera were the most frequent prey items. In a study of Charadriiform chick diet in The Netherlands, Lapwing chicks were found to specialise on earthworms, Coleoptera and Tipulid larvae (Beintema *et al.*, 1991). Furthermore, a steady increase with age in the number of earthworms consumed was recorded and the study

suggested that chicks switch to more energetically profitable prey items (earthworms) to meet increased daily energy requirements as chicks grow older.

Given the significance of earthworms to the breeding behaviour of adult Lapwings and as a food source for chicks, it is important to know how earthworm populations are affected by different agricultural practices. A number of widespread agricultural practices are known to have a detrimental effect on earthworm numbers and densities. The four main management inputs into any farming system can be summarised as cultivations, cropping patterns, fertilisation and crop protection (Edwards & Bohlen, 1996), this chapter presents data investigating the first two of these.

Cultivation is known to have detrimental effects on earthworm populations. Continued cultivation may lead to a reduction in organic matter and food availability for earthworms, allow predators such as birds easier access to earthworms when bought to the surface, and also through direct mortality through the cultivation process (Edwards & Bohlen, 1996). Furthermore the type of cultivation is important. Edwards & Lofty (1978) have shown that earthworm populations and biomass were much higher in direct-drilled than in conventional mould-board ploughed plots. Cropping patterns can also have a strong influence on the numbers of earthworms that are available within agricultural land. It is well established that grassland habitats contain more earthworms than arable land (Svendsen, 1957) and pastures are important as a feeding habitat for both adult Lapwings and their chicks. In an arable context, long-term study plots at Rothamsted Experimental Station, showed that earthworm biomass was greatest under continuous cereals, with lower populations under root crops (Edwards & Bohlen, 1996). Although beyond the scope of this work, in their comprehensive review of the indirect effects of pesticides on birds, Campbell *et al.* (1997) show that most invertebrate groups associated with farmland have declined or stabilised in the last 20-30 years. Furthermore, for a number of declining farmland birds, downward trends correlate with a period of increasing pesticide use. Although it adds to the evidence of an indirect effect of pesticides, it does not imply a causal relationship. Most pertinent to Lapwings are the known detrimental effects of Carbamate fungicides and the molluscicide Methiocarb which have been shown to be toxic to earthworms (Edwards, 1984: Bieri *et al.*, 1989). Detailed experimental

work is currently being undertaken to investigate the possible effects that pesticides may be having on bird populations (Morris, 2002).

The aims of this chapter are:

i) to identify the important components of Lapwing chick diet, and to identify spatial and temporal trends, with a particular emphasis on earthworms,

ii) to investigate some of the factors that affect earthworm abundance in arable farmland,

iii) to suggest a number of mechanisms that could be incorporated into general agricultural practice or into agri-environment schemes to have possible benefits to breeding Lapwings in relation to increased earthworms

6.2 METHODS

6.2.1 Earthworm sampling

Soil cores were taken using a soil corer 10cm in diameter by 10cm depth. Ten samples were taken from random positions within the central area of fields. All the samples were transferred to the same plastic bag and returned to a laboratory where they were processed within 48 hours. The samples were hand sorted by carefully teasing apart the soil using tweezers. All worms were separated from the soil and washed to remove excess dirt. All worms from each field sampled were dried on blotting paper at room temperature for thirty minutes. The sample of worms was then weighed to give a total weight per field per sampling period.

Samples were collected from seven crop types: winter wheat (n=9), winter beans (n=3), spring barley (n=11), sugar beet (n=2), potatoes (n=3), set-aside (n=7) and Option 1B (n=10), pasture (n=6), where n=number of fields. Winter cereals and beans were combined to give an all winter cultivation estimate of earthworm biomass, and spring barley, potatoes and sugar beet were similarly combined in to an all spring cultivation category. The fields were selected prior to the onset of breeding, and did not necessarily have Lapwing territories on them. Repeat samples were

taken four weeks apart, over four sampling periods extending from 1st March to 5th June. Winter crops were not monitored during the final sampling period, primarily due to the likelihood of damage to the crop. Spring crops were not necessarily drilled prior to the first sampling round as many cultivations had not been completed. Earthworm biomass was converted into g/m^{-2} to allow direct comparison between fields and study areas.

Earthworm sampling was undertaken in the Shropshire study area in 2000 only. Supplementary data were also collected from the Cambridge area in 1999.

6.2.2 Faecal analysis

Faecal samples were collected from chicks whilst taking biometric data during survival studies of ringed chicks (see Chapter 5). In 1999 a small number of samples were collected primarily to assess the feasibility of using faecal analysis to investigate diet preference. Data were collected from Shropshire and Cambridge study areas. The limited nature of the study allowed only a small number of samples to be collected, and thus, only the presence or absence of major taxonomic groupings of invertebrate prey items were recorded.

In 2000 a larger number of faecal samples were collected in the Shropshire study area to allow a more comprehensive analysis of chick dietary content. All samples were stored in 70% alcohol in a small glass collecting tube with an airtight lid. A 115mm Petri-dish was adapted by gluing a smaller 75mm Petri-dish centrally within the larger dish to form a 20mm wide annular channel. The underside of the larger dish was inscribed with radial lines at 10° intervals so that the annulus was divided into 36 equal sectors (Green & Tyler, 1989). The faecal sample was teased apart and spread evenly throughout the channel so each of the 36 sectors had some component of the sample. Using a 30× magnification binocular microscope the contents of the channel was searched and fragments of prey items identified using photographs and descriptions of diagnostic features outlined in Moreby (1988). For arthropods, all fragments in each of the 36 sectors were identified, counted and recorded. The number of fragments found in each sample were converted to the number of whole animals eaten by multiplying by the correction values (k) given in Galbraith (1989b) (Table 6.1). Minimum numbers of individuals eaten for less common taxa such as

Formicidae and Aphidae were estimated by dividing the number of fragments found by the number of component parts per animal. In all instances the number of individuals eaten were rounded up to the nearest whole number. Earthworm chaetae can be very numerous (Green & Tyler, 1989) and so were counted in a sub-sample of every sixth sector of the 36 sectors. No attempt was made to estimate the number of individual worms eaten, instead it was expressed as the number of chaetae per gram of faecal sample. Once the alcohol solution had completely evaporated the dry weight for each faecal sample was recorded.

Temporal changes in diet preferences in relation to chick age were investigated by categorising chicks in two ways, i) chicks into 3 arbitrary age categories, 0-11,12-23, and >24 days old, and ii) chicks age regressed on to the relevant dietary component.

Table 6.1. Correction factors (*k*) used in the calibration of parts found in faecal samples (from Galbraith 1989b).

	k
Coleoptera mandibles	1.3
Coleoptera femora	1.2
Coleoptera tibia	1.1
Coleoptera larvae-mandible	1.1
Spider chelicera	1.0

6.2.3 Chick growth rate

Chick growth rate was estimated for chicks for which there were two faecal samples collected at least 2 days apart, and for which there was corresponding biometric data. The growth rate was calculated for each individual chick using the equation:

weight (day 2) – weight (day 1) / number of interval days

The mean number of earthworm chaetae and Coleoptera per gram of faecal sample, average chick age and average date the measurements/faecal samples were collected, were calculated and treated as explanatory variables. GLIM 3.77 was used to model growth rate using normal errors and an identity link (Crawley, 1993). The maximal model was fitted and all explanatory variables were deleted in turn to assess the significance of the term in respect to the reduction in deviance. The variable explaining the least amount of deviance was dropped if it was non significant. The only terms left in the final model were significant. Quadratic terms were also fitted to detect non-linear relationships with the response variable (ie growth rate). The goodness of fit of the final models were assessed by plotting standardised residuals against the standard normal cumulative distribution function using the MCHECK macro from Crawley (1993).

6.2.4 Soil moisture deficit

Soil moisture deficit (SMD) was determined as previously described in Chapter 2.2.1.

During 2000 a new method of investigating soil moisture in relation to Lapwing chick foraging was trialed using the *ThetaProbe* Type ML2x (Delta-T Devices Ltd.), which gives an instantaneous measure of volumetric soil moisture content. Volumetric soil moisture content is the ratio between the volume of water present and the total volume of the sample, expressed as $m^3.m^{-3}$. Ten measurements were randomly taken approximately within 5m of the foraging chick. A further ten measurements were taken randomly within the same field. An independent *t*-test was used to investigate the hypothesis that chicks were foraging in areas with a higher soil moisture content than random points with in the same field. Shapiro Wilks and Levene's test were used to check for normality and homoscedasticity respectively.

6.3 RESULTS.

6.3.1 Earthworm abundance

Earthworm biomass differed according to crop type and tended to decline as the Lapwing breeding season progressed (Table 6.2). Initial measurements at the start of the breeding period showed a large difference in earthworm biomass density between crop types (Kruskal Wallis, H=12.93, 4 df, P=<0.01) (Figure 6.1). Much of this difference was attributable to differences between pasture and other crop types; 1B (Mann Whitney U=4.0, P=<0.05), winter cultivation (Mann Whitney U=1.0, P=<0.01), and spring cultivation (Mann Whitney U=8.0, P=<0.05). All other differences were non-significant.

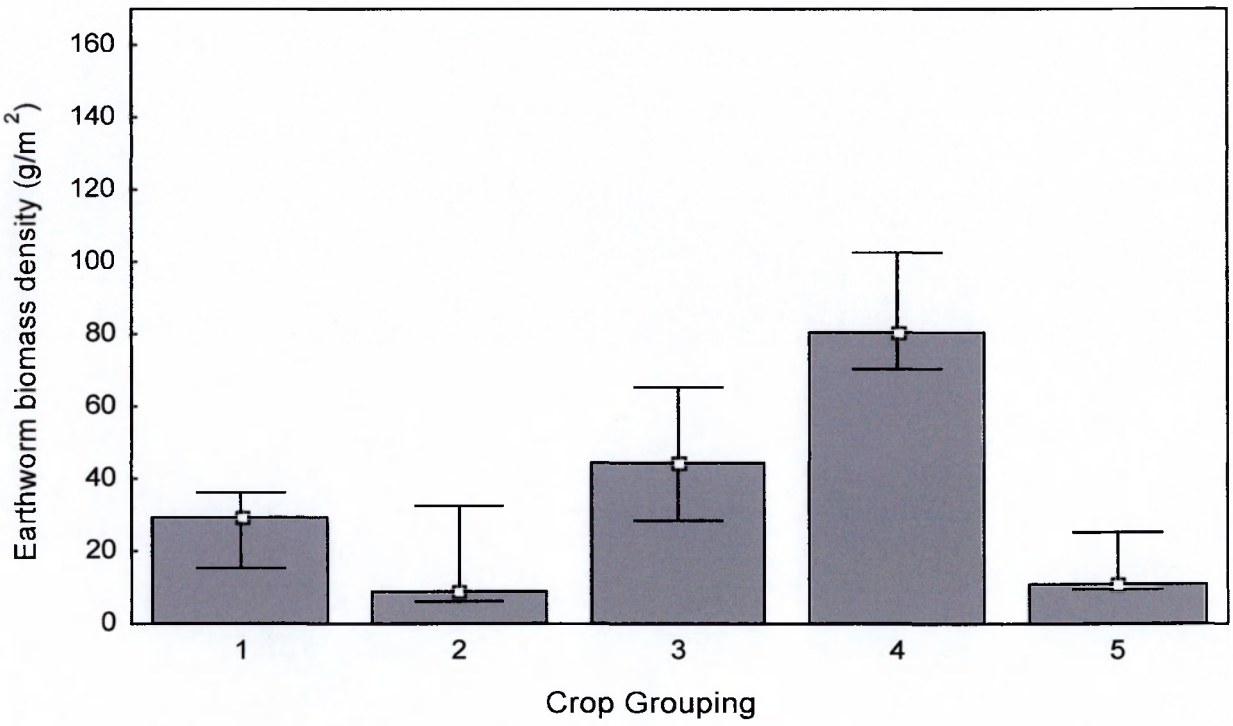

Figure 6.1. Median earthworm biomass density (g/m^{-2}) by crop groupings sampled during period 1 (1-10 March). Where, 1=Option 1B, 2=winter cultivation, 3=rotational set-aside, 4=pasture, 5=spring cultivation. Winter cultivation includes cereals and beans, and spring cultivations include cereals, stubbles sugar beet and potatoes. There is a significant difference in earthworm biomass density between crop groupings (Kruskal Wallis, H=12.93, 4 df, P=0.012). Error bars show the interquartile range

Table 6.2. A summary of earthworm biomass density by crop categories during 4 sampling periods, where period 1=1-10 March, period 2=3-10 April, period 3=1-8 May, and period 4 =1-5 June. Columns in italics denote the periods that coincide with chick foraging. Mean biomass density (g/m^{-2}) is given with associated standard error value, *n*=the number of fields sampled during each of the sampling periods. Winter cultivation includes cereals and beans, and spring cultivations include cereals, sugar beet and potatoes. Note, in period 1 spring cereals, potatoes, sugar beet and Option 1B categories include stubble fields prior to cultivating and/or drilling.

	Period 1		Period 2		*Period 3*		*Period 4*	
	n	Mean biomass density (g/m^{-2}) ±SE	*n*	Mean biomass density (g/m^{-2}) ±SE	*n*	*Mean biomass density (g/m^{-2}) ±SE*	*n*	*Mean biomass density (g/m^{-2}) ±SE*
Winter cereal	7	15.9±5.9	9	30.4±11.8	*9*	*37.3±14.3*	-	-
Winter beans	-	-	3	19.6±19.2	*3*	*4.0±3.5*	-	-
All win. cultivation	7	15.9±5.9	12	27.7±9.7	*12*	*29.0±11.5*	-	-
Spring cereals	7	53.9±5.3	11	14.3±4.1	*11*	*9.5±4.3*	*11*	*8.9±3.8*
Potatoes	3	8.8±4.9	3	17.7±3.8	*3*	*8.1±6.3*	*3*	*13.4±5.7*
Sugar beet	2	5.6±5.6	2	0	*2*	*5.4±5.4*	*2*	*10.2±2.8*
All spr. cultivations	12	34.6±15.9	16	13.2±3.1	*16*	*8.7±3.1*	*16*	*9.9±2.7*
Option 1B	7	33.2±8.6	10	23.5±3.7	*10*	*35.5±8.0*	*10*	*20.1±7.9*
Permanent pasture	4	99.9±16.7	6	154.7±27.0	*6*	*115.4±31.7*	*6*	*59.6±24.2*
Temporary grass	2	17.3±17.3	2	28.3±26.3	*2*	*13.2±13.2*	*2*	*1.7±1.7*
Set-aside (cereal)	3	46.2±10.6	7	39.7±12.5	*7*	*48.0±14.6*	*6*	*14.6±5.2*
TOTAL	35	38.1±7.3	53	38.5±7.2	*53*	*35.4±6.5*	*40*	*20.2±4.9*

Ten fields were sampled during the first sampling round prior to cultivation and were subsequently cultivated before sampling round 2. The earthworm biomass density following cultivation declined for all ten fields, and the mean biomass density was significantly lower following cultivation ($F_{1,18}$=10.2, P=<0.005) (Figure 6.2). Data was log transformed to improve normality.

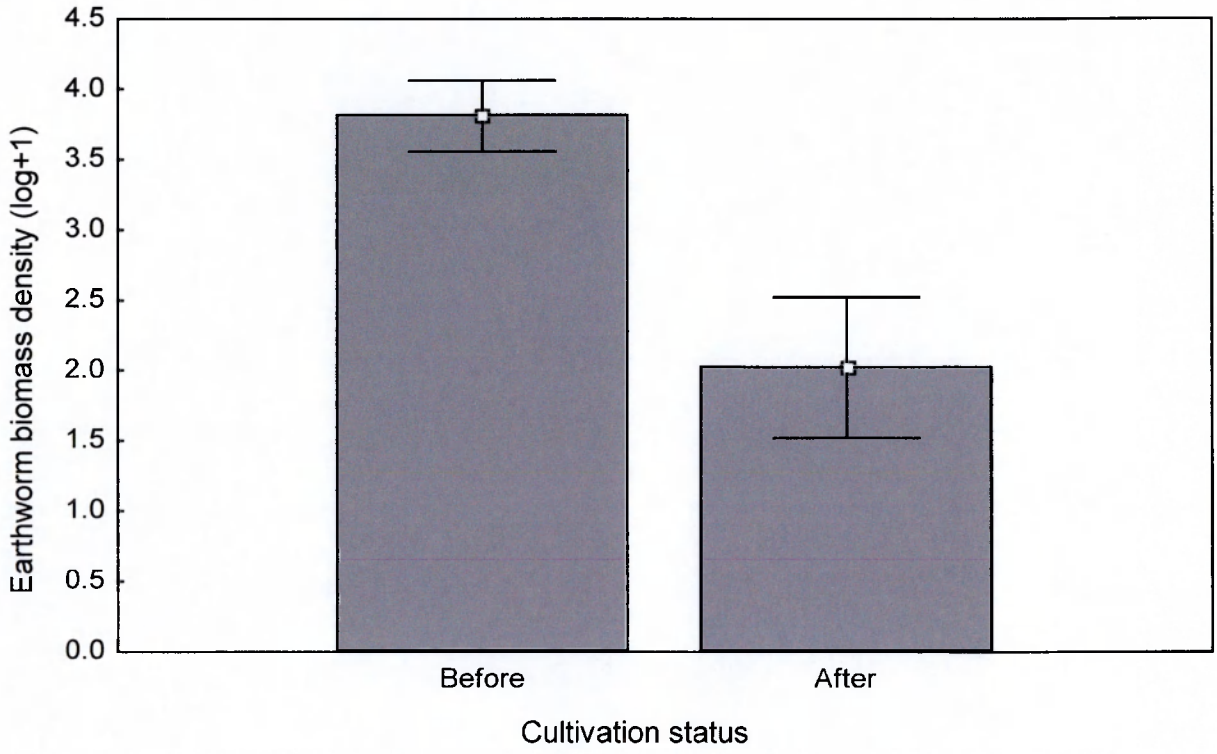

Figure 6.2. Earthworm biomass density (g/m^{-2}) in fields that were sampled both before and after cultivation. Biomass density was significantly lower following cultivation, $F_{1,18}$=10.2, P=<0.005. Bars denote one standard error.

There was no apparent difference between earthworm biomass density in Option 1B and spring cereal fields ($F_{1,11}$=3.84, P=0.076) although the difference approached significance. However, there was a significant difference between crop type over time ($F_{3,33}$=3.37, P=0.046) (Figure 6.3), which is attributable to a slower rate of decline in earthworms on Option 1B fields when compared to spring cereals ($F_{1,11}$=6.27, P=0.029).

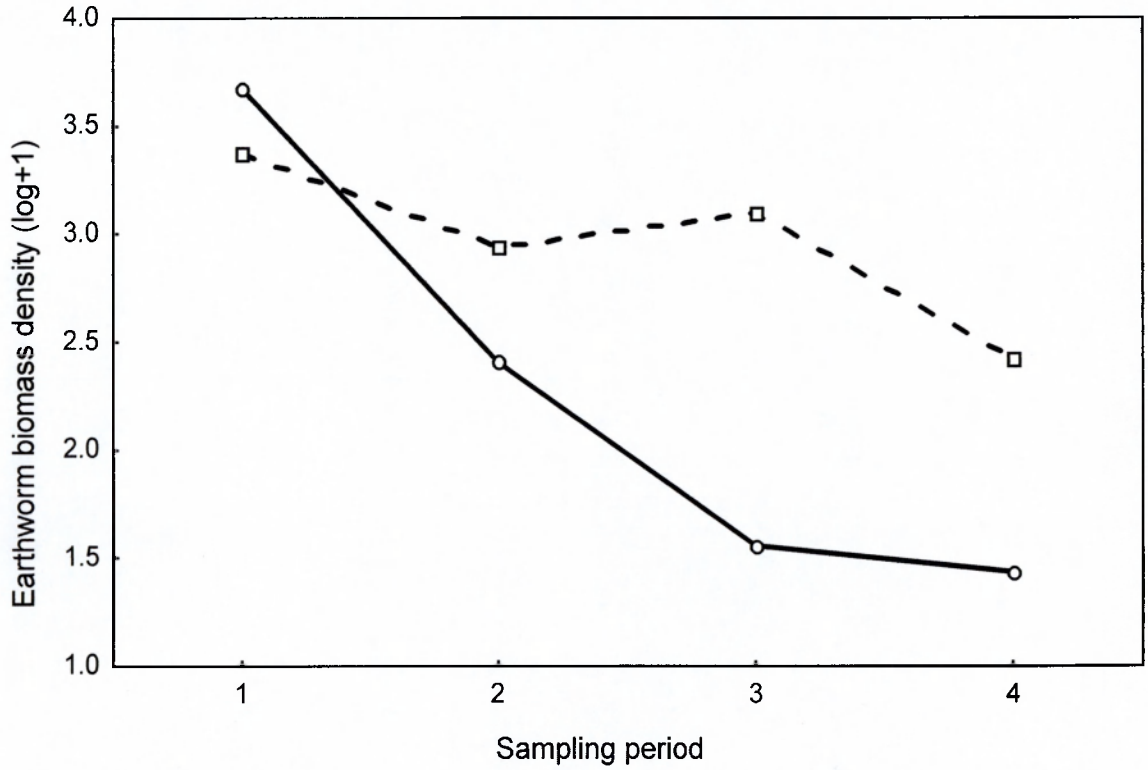

Figure 6.3. A comparison of the change in earthworm biomass density (g/m^{-2}) between Option 1B (dashed line) and spring cereal (solid line) fields (see text for details). Where, period 1=1-10 March, period 2=3-10 April, period 3=1-8 May, and period 4 =1-5 June.

In the Shropshire study area for 2000 there was no significant effect of soil moisture deficit on earthworm biomass ($F_{1,138}$=2.77, P=0.098), but there was a significant effect in the Cambridge study area in 1999 ($F_{1,31}$=51.95, P=<0.001) (Figure 6.4).

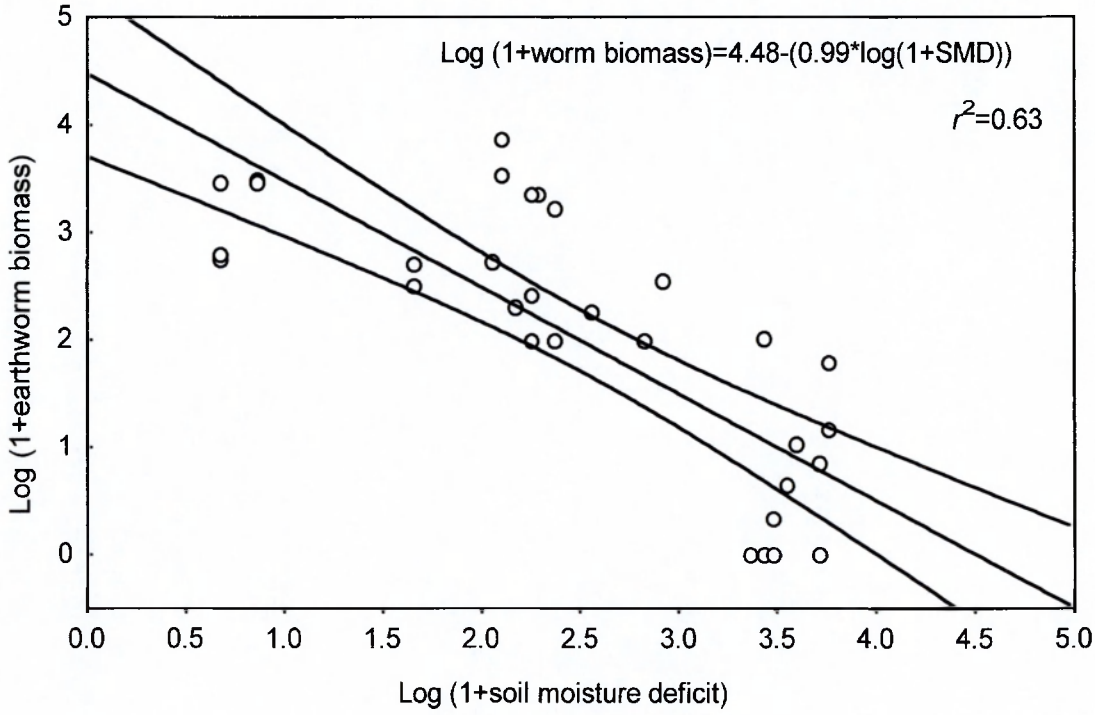

Figure 6.4. Earthworm biomass density (g/m^{-2}) in relation to calculated soil moisture deficit for the Cambridge study area in 1999. The fitted regression model (solid line) with 95% confidence limits (dashed line) is shown.

6.3.2 Faecal analysis

In 1999 a small number of samples were collected from chicks in Cambridge (n=6) and Shropshire (n=13). The percentage occurrence of invertebrate groupings are given in Table 6.3, the most common prey items in both study areas were Coleoptera and earthworms. Aranae were not present in any of the samples from Cambridge but occurred in 62% of samples from the Shropshire study site. Contrastingly, Diptera were more common in the Cambridge samples.

Table 6.3. Percentage occurrence of major taxonomic groupings identified in faecal samples collected from Lapwing chicks in 1999, from Shropshire and Cambridge study areas.

	n	Coleoptera	Annelid	Aranae	Diptera	Aphid	Mollusc
Shropshire	13	77%	85%	62%	23%	31%	23%
Cambridge	6	100%	67%	-	83%	-	17%
Overall	19	84%	79%	42%	42%	21%	21%

From the 2000 field season a total of 87 faecal samples were collected and analysed for invertebrate content. Of these, 9 samples were excluded from the analysis because they were collected from chicks that were located in the nest scrape. These chicks were unlikely to have been feeding, and so contained very few fragments. Samples were collected from chicks in a variety of habitat types: Option 1B, n=12; set-aside, n=24; grass, n=21; spring crops, n=15; and others, n=6 (Table 6.4).

The most common major prey items found in the faecal samples were earthworms (94% of samples), Coleoptera (94% of samples) and Aranae (72% of saamples), and sample sizes allowed further analyses.

Table 6.4. Frequency of occurrence (and percentages) of major taxonomic groupings identified in faecal samples collected in 2000 *(n*=78). The crop type 'grass' includes reseeded grass leys, permanent pasture and set-aside grass; 'spring crops' includes sugar beet, spring beans, and spring cereal; and 'others' includes winter cereals, potato stubble and cereal stubble. Abbreviations of taxonomic groupings are as follows: Anne=annelids; Coleo=All Coleoptera; Carab=Carabidae; Curc=Curculionidae; Chrys=Chyrsomelidae; Staph=Staphylinidae; Elat=Elateridae; Scarab=Scarabadae; Larvae=Coleopteran larvae; Aran=Aranae; Dipt=Diptera, Sawf=sawfly larvae; Formi=Formicidae; Aphid=Aphidae, and Mollus=Molluscidae.

Crop type		Anne	Coleo	Carab	Curc	Chrys	Staph	Elat	Scarab	Larvae	Aran	Dipt	Sawf	Formi	Aphid	Mollu
All habitats	*f*	73	73	61	52	13	15	4	10	23	56	35	10	5	17	21
(*n*=78)	%	94	94	78	67	17	19	5	13	29	72	45	13	6	22	27
Set-aside	*f*	21	23	16	15	7	5	1	1	5	18	16	1	4	10	6
(*n*=24)	%	88	96	67	63	29	21	4	4	21	75	67	4	17	42	25
1B	*f*	12	11	10	6	1	3	-	1	4	9	4	1	-	4	6
(*n*=12)	%	100	92	83	50	8	25	-	8	33	75	33	8	-	33	50
Grass	*f*	20	20	16	15	2	2	-	5	11	14	8	8	-	-	7
(*n*=21)	%	95	95	76	71	10	10	-	24	52	67	38	38	-	-	33
Spr crops	*f*	14	13	13	12	3	3	1	2	-	11	6	-	1	2	1
(*n*=15)	%	93	87	87	80	20	20	7	13	-	73	40	-	7	14	7
Others	*f*	6	6	6	4	-	2	2	1	3	4	2	-	-	1	1
(*n*=6)	%	100	100	100	67	-	33	33	17	50	67	33	-	-	17	17

6.3.2.1 *Coleoptera*

The number of Coleoptera found in faecal samples collected from chicks of different ages was significantly different ($F_{2,75}$=3.42, P=0.04), with the youngest chicks (1-11 days) taking more Coleoptera than older chicks (24+), (Newman Keuls *post hoc* test, P=0.04) (Figure 6.5).

A linear regression of chick age against the mean frequency of Coleoptera present shows a significant negative relationship, $F_{1,76}$=6.16, P=0.015. However, there was no significant effect of number of Coleoptera on chick condition, $F_{1,76}$=0.81, P=0.37.

The number of Coleoptera recorded in faecal samples declined in relation to the date the sample was collected $F_{1,76}$=5.66, P=0.0199.

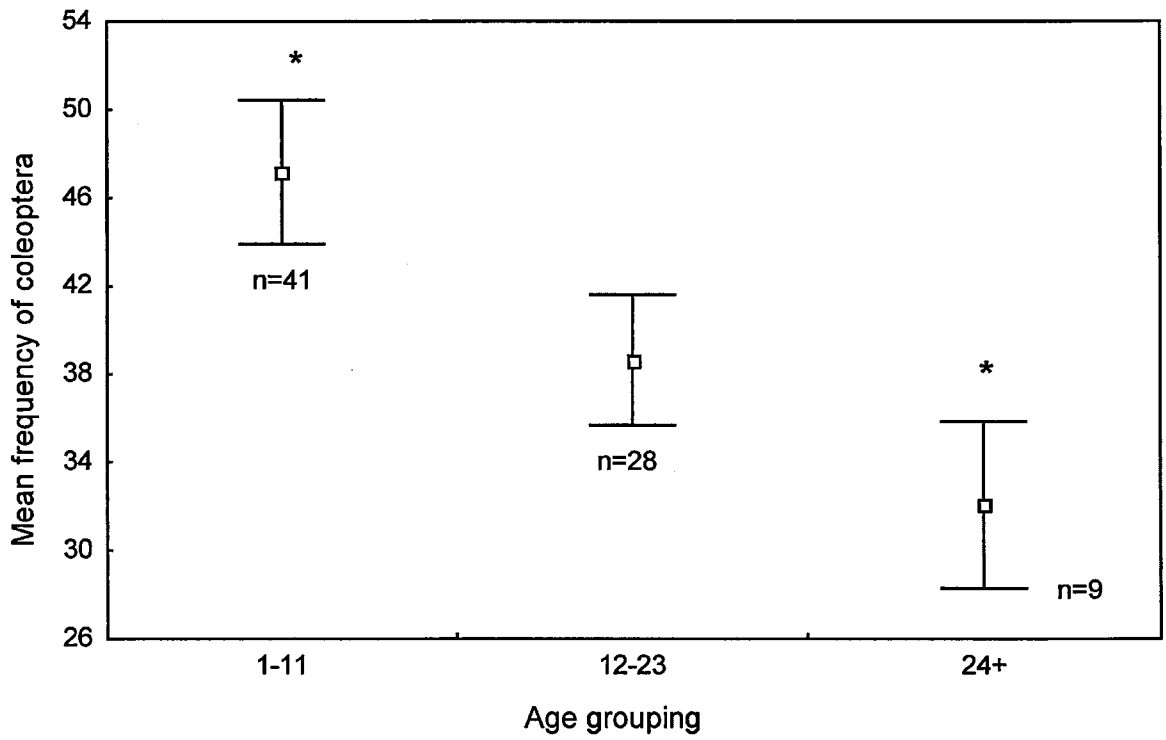

Figure 6.5. The frequency of Coleoptera in faecal samples by age grouping. There is a difference between age categories, $F_{2,75}$=3.42, P=0.04, groups with asterisks are significantly different from each other. Mean values are shown with one standard error.

6.3.2.2 *Aranae*

There was a significant difference in the number of Aranae found in faecal samples of chicks of different ages (Kruskal Wallis $H_{2,78}$=7.22, P=0.03), with the young chicks (1-11 days) having a greater frequency of Aranae in samples than chicks aged 12-23 days old (Mann Whitney U=359.5, P=0.009) (Figure 6.6).

A linear regression of chick age against mean frequency of Aranae present in faeces shows a significant negative relationship ($F_{1,76}$=6.65, P=0.01). There was no significant effect of Aranae on chick condition, $F_{1,76}$=0.91, P=0.34.

The number of Aranae recorded in faecal samples declined (non significantly) in relation to the date the sample was collected ($F_{1,76}$=0.006, P=0.94). Note the variable (frequency of Aranae per gram) was log transformed to improve linearity.

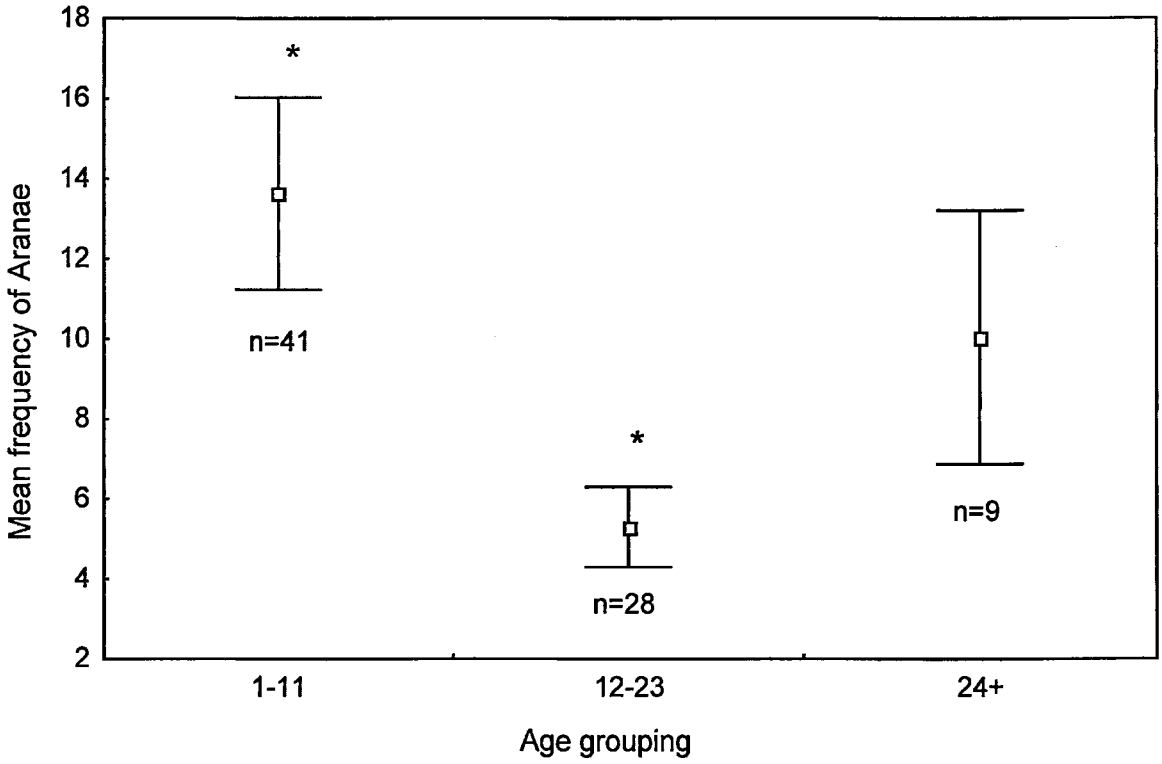

Figure 6.6. The frequency of Aranae in faecal samples by age grouping. There is a significant difference between age categories, Kruskal Wallis $H_{2,78}$ P=0.03, groups with asterisks are significantly different from each other. Mean values are shown with one standard error.

6.3.2.3 *Earthworms*

The number of earthworm chaetae found in faecal samples collected from chicks of different age class are significantly different, Kruskal Wallis $H_{2, 78}$=27.5, P=<0.0001. Chicks from age class 1-11 days, have a greater frequency of chaetae than those chicks aged 12-23 days (Mann Whitney U=189.0, P=<0.0001) and 24+ (Mann Whitney U=51.0, P=<0.001) (Figure 6.7).

There is a significant positive relationship between the age of the chick and the number of chaetae per gram of faecal samples $F_{1,76}$=51.7, P=<0.0001 (Figure 6.8). Furthermore, there is a significant positive effect on the frequency earthworm chaetae on chick condition, F=61.42$_{1,76}$, P=<0.0001, (Figure 6.9).

There was no significant relationship between chaetae per gram and the day the sample was collected, $F_{1,76}$=0.58, P=0.45.

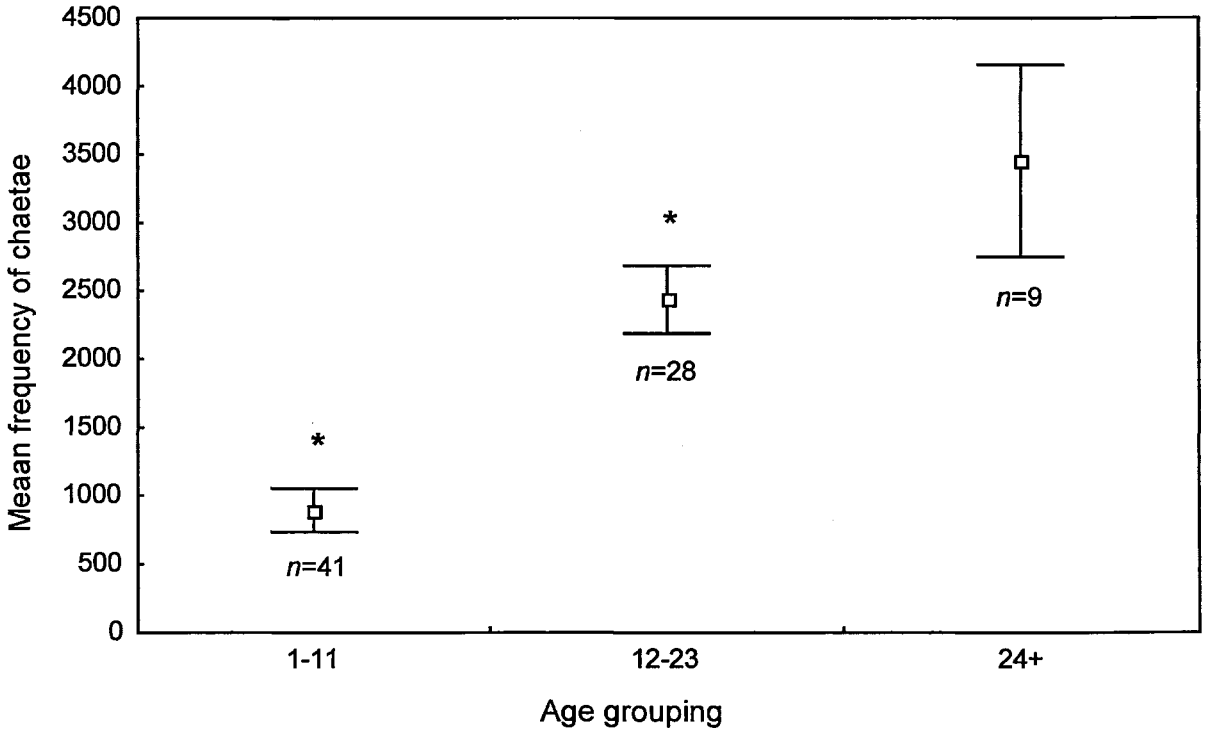

Figure 6.7. The frequency of earthworm chaetae in faecal samples by age grouping. There is a difference between age categories, Kruskal Wallis $H_{2,78}$=27.5, P=<0.0001, groups with asterisks are significantly different from each other. Mean values are shown with one standard error.

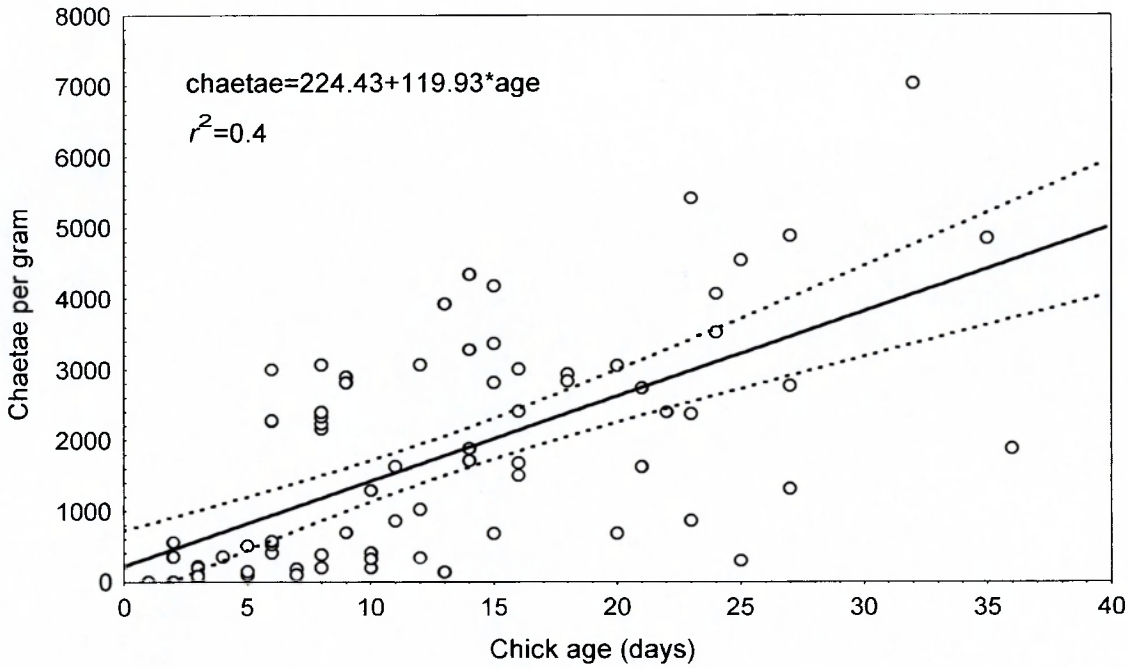

Figure 6.8. The number of chaetae per gram of faecal sample in relation to chick age. The solid line represents the fitted regression model, with 95% confidence limits (dashed lines).

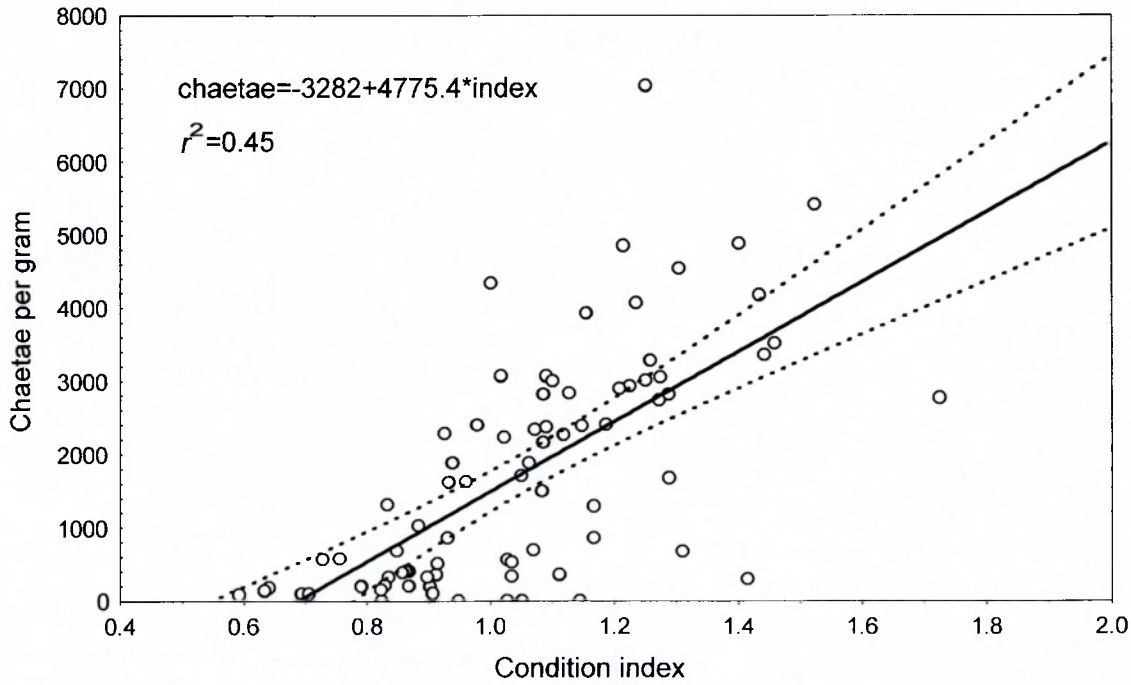

Figure 6.9. The number of chaetae per gram of faecal sample in relation to chick condition index. The solid line represents the fitted regression model, with 95% confidence limits (dashed lines).

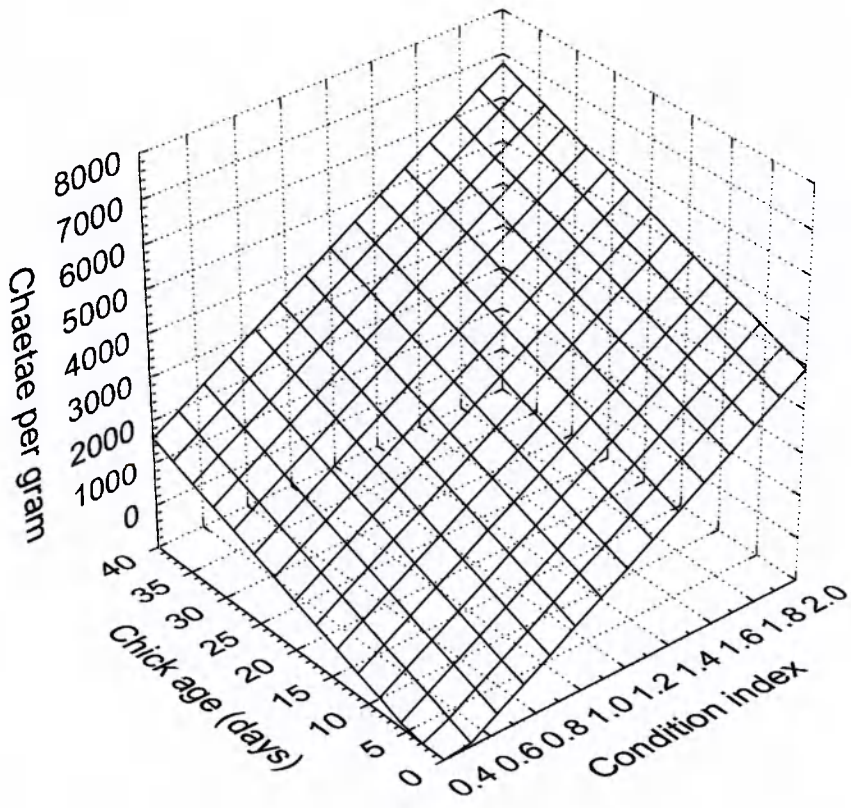

Figure 6.10. The influence of chick age and body condition on the quantity of earthworm chaetae found in faecal samples. See text for model equation.

The variables chick age and condition index are positively correlated Pearson's r=0.56, P=<0.001). Despite this, when both variables are combined in a multiple regression analysis both are retained (Figure 6.10) to give the following model:

Chaetae per gram=-2584.98 + (3247.8*condition index) + (71.88*chick age)

F=45.22$_{2,75}$ P=<0.0001 (r^2=0.55).

During the 2000 breeding season, chicks were present from 18th April (day 108) until 24th July (day 205), with the first faecal samples being collected on 20th April (day 110) and the final sample on 28th June (day 179). Despite differences in earthworm biomass between crop type (Table 6.2 and Figure 6.1). There was no difference in the median number of earthworm chaetae in faecal samples collected from a variety of crop types (Kruskal Wallis $H_{4,77}$=9.26, P=0.055) (Figure 6.11). The correlation between the number of earthworm chaetae and the number of Coleoptera in faecal samples was weak (Pearson's r=-0.1, P=0.37).

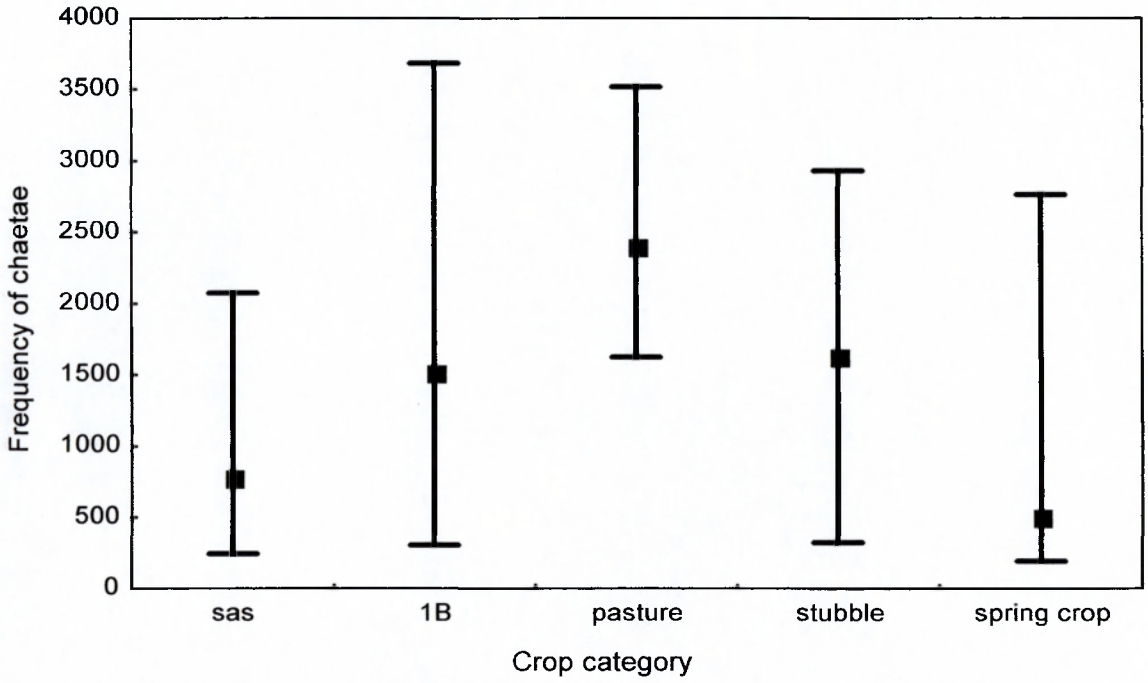

Figure 6.11. The number of earthworm chaetae per gram in relation to the crop type on which the faecal sample was collected. Medians with the interquartile range are shown.

6.3.3 Chick foraging and soil moisture relationships

A total of 13 sets of measurements were collected from 9 different chicks on 3 different days (Table 6.5). Of these, 10 sets of measurements show that chicks were foraging in areas with higher soil moisture measurements that random measurements taken within the same field.

Table 6.5. Mean soil moisture readings ($m^3.m^{-3}$) in areas where chicks were seen to be foraging compared to random measurements taken within the same field. The *t*-value is given with associated degree of significance, *=<0.01, **=<0.001. All soil moisture measurements were taken with a *ThetaProbe* (see text for details). Chick ID refers to the chick radio-tag number.

Chick ID	Date	Mean moisture ($m^3.m^{-3}$) (foraging area)	Mean moisture ($m^3.m^{-3}$) (random area)	*t*-value
235	4/5	0.19	0.121	3.57*
253	4/5	0.213	0.121	3.37*
423	4/5	0.439	0.398	3.44*
553	4/5	0.435	0.398	3.76*
463	10/5	0.369	0.186	9.49**
235	10/5	0.104	0.103	0.08 n.s.
253	10/5	0.174	0.103	3.49*
501	10/5	0.268	0.258	0.61 n.s.
782	10/5	0.415	0.326	3.96*
553	11/5	0.287	0.141	6.14**
268	11/5	0.341	0.364	-1.21 n.s.
771	11/5	0.399	0.137	10.52**
423	11/5	0.314	0.256	2.77*

6.3.4 Chick growth rate

Data for 19 chicks from 19 different broods (to avoid non-independence of data and pseudo-replication) allowed analysis of dietary content in relation to growth rates.

The number of earthworm chaetae was retained in the MAM ($F_{1,17}$=28.24, P=<0.01) as was the quadratic function ($F_{1,17}$=27.86, P=<0.05), resulting in the final model:

$$\text{Chick growth rate} = -5.49^{-7}*\text{chaetae}^2+0.0034*\text{chaetae}+1.516$$

The final model accounted for 61% of the deviance of the null model. Fitted model values are given in Figure 6.12. There was no significant effect of Coleoptera on growth rates, $F_{1,17}$=0.4, ns.

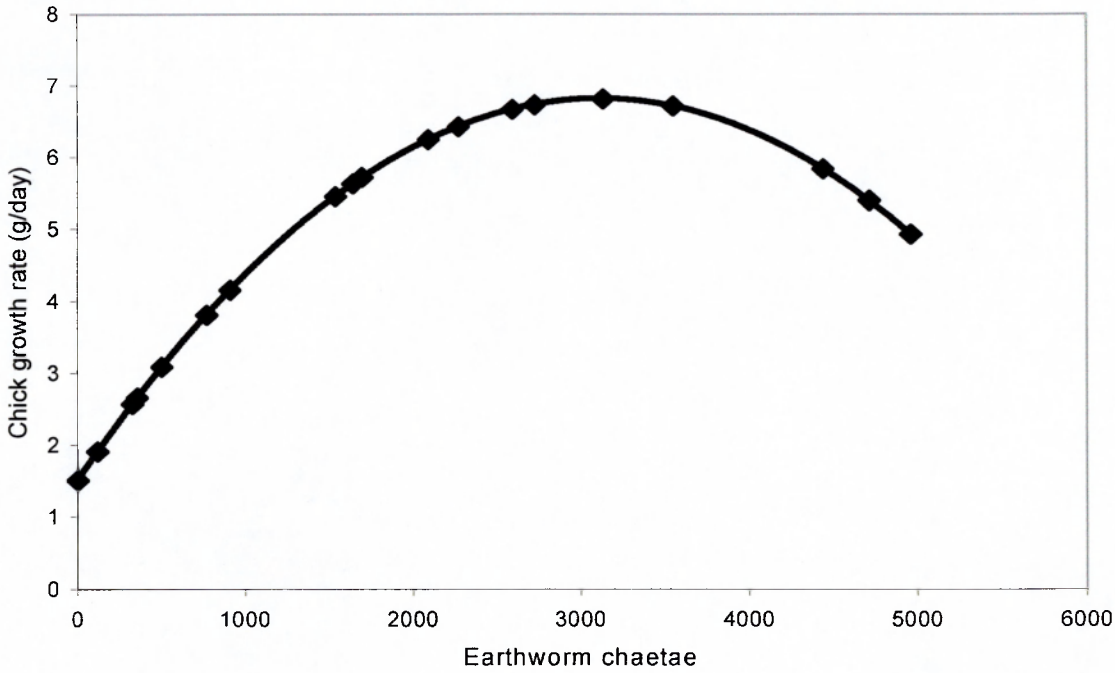

Figure 6.12. Model fitted values for growth rates of chicks versus earthworm chaetae, incorporating the linear and quadratic forms of the number of earthworm chaetae per gram of faecal sample.

6.4 DISCUSSION

6.4.1 Earthworm abundance and agricultural practice

Two of the most important factors affecting the availability of earthworms to Lapwings in agricultural soils are the amount of organic matter near the soil surface and the length of time since cultivation (Edwards & Bohlen, 1996). Data on organic content of soils were not collected as part of this study, although the detrimental effects of cultivations were apparent. Earthworm biomass densities were greatly reduced in fields sampled soon after cultivation compared to samples taken beforehand. Experimental work by Edwards & Lofty (1978) concluded that the most important effects on earthworm populations were indirect, due to the incorporation of surface litter into the soil, resulting in a loss of insulating cover on the soil surface and the redistribution of organic food sources.

The less marked negative effect on earthworm biomass of shallow cultivation associated with Option 1B fields in comparison with conventionally ploughed spring cereals, confirms previous work that suggests that moderate cultivation (such as discing) favoured earthworms by loosening the soil (Zicsi, 1969). Hence, the availability of earthworms is greater than on ploughed spring cereal and the decline throughout the Lapwing breeding season is more gradual. The presence of organic surface debris on Option 1B may increase earthworm activity near the surface of the soil, making them more available to Lapwing chicks and adults. Similarly, many studies of the effects of direct drilling on earthworm populations have shown the practice to be very beneficial for earthworms (Edwards & Bohlen, 1996; Edwards & Lofty, 1982a; Barnes & Ellis, 1979). Another of the most important factors controlling earthworm populations in arable land is the amount of organic matter that is available as food (Evans & Guild, 1948; Edwards & Bohlen, 1996). Applications of bulky organic manures, such as farmyard manure, increase earthworm populations in soils quite rapidly (Curry, 1976) and although artificial nitrogenous fertilisers have similar effects, these are more limited (Edwards & Lofty, 1982b; Tucker, 1992; Edwards & Bohlen, 1996). In general, the decreased use of farmyard manure and the increased use of fast acting artificial fertiliser, has led to a decrease in diversity and size of most soil invertebrate populations

in arable land (Edwards, 1984). In grassland habitats a large amount of organic matter exists naturally in the soil, and although the application of manures will not necessarily increase the already high invertebrate densities, they may lead to an increase in earthworm surface activity (Scullion & Ramshaw, 1987) making them more readily available to foraging Lapwings.

The influence of soil moisture on earthworm biomass is well documented (Wood, 1974). The lack of a relationship between SMD and earthworm biomass in the Shropshire study area in 2000 was most likely due to the lack of any prolonged period of dry weather conditions, and was further compounded by all the sampling periods being during times of low SMD (see Appendix 2). In fields where SMD remains low, earthworm activity near the soil surface may increase their availability to Lapwing chicks and adults. There is likely to be an interaction between SMD and the quantity of organic matter near the soil surface, but this was not investigated in this study, and requires further research in the context of increasing worm availability as a food source for Lapwings (and other farmland birds).

In long-term study plots at Rothamsted Experimental Station, earthworm biomass was greatest on continuous cereals, with lower populations under root crops (Edwards & Bohlen, 1996). It is well established that grassland habitats contain more earthworms than arable land (Svendsen, 1957) and pastures are important as a feeding habitat for both adult Lapwings and their chicks. Consequently access to pasture from an arable nesting site can be a critical factor in increasing chick survival (Galbraith, 1988a). Hence a mosaic of crop types and management practices offer the best potential conditions for Lapwings breeding on lowland farmland.

To summarise, in an arable context two agricultural practices that may have potential benefits are minimal tillage/direct drilling methods and inputs of organic manures. Minimal tillage is unlikely to be incorporated into agri-environment schemes but may become increasingly utilised in the future as a method of reducing inputs and on-farm costs. Current research is underway to assess the effect of minimal tillage on food resources for birds (Cunningham, 2002). Increasing organic manure inputs should have potential benefits in terms of increasing organic matter content within soils, and stimulating sub surface activity of earthworms (Scullion & Ramshaw, 1987) thus increasing their availability to Lapwing chicks and adults.

6.4.2 Lapwing chick diet

This study, in agreement with previous work (Galbraith 1988a, 1989b; Beintema *et al.* 1991; Linsley 1999) shows the diet of Lapwing chicks to be generally varied with a predominance of certain taxonomic groups, primarily earthworms, Coleoptera and Aranae. Although Matter (1992) found that earthworms were present in very small numbers this may be due to his sample consisting of stomachs from chicks aged between 2-8 days, an age when earthworms may not be a major constituent of the diet. Differences in diet composition between various studies almost certainly reflect underlying differences in invertebrate availability and abundance, reflecting climatic, geographic and habitat specific effects. However, in contrast to previous work there is some evidence that Lapwing chicks were feeding selectively on earthworms rather than adopting an opportunistic foraging strategy as proposed by Galbraith (1989b). Earthworm abundance in faecal samples collected later in the breeding season did not show a decline despite a general decrease in earthworm availability. Indeed the period where decline in earthworm availability is most apparent (between period 3 and 4) coincides with the main chick foraging period. Furthermore, despite the low abundance of earthworms on Option 1B and spring cultivated fields, there was no evidence to suggest that earthworms were comprising substantially less of the diet when compared to pasture fields (that had up to ten times greater earthworm biomass (Table 6.2; Figure 6.10)).

Furthermore, the importance of earthworms in chick diet is highlighted by the positive relationships with chick age, body condition and daily growth rates, suggesting that chicks are increasingly reliant on earthworms as they develop. Although the increase in worms in faecal samples with age could be due to larger stomach volume, this would be difficult to ascertain without post mortem analyses. Earthworms are known to be a favoured food for adults in the pre-breeding season primarily due to their high calorific value (Högstedt, 1974), and a similar strategy of optimising calorific intake for chicks, may well help meet dietary needs in relation to physiological growth. Calculations of daily food requirements for captive Lapwing chicks suggest that near fledging chicks are unable to meet energy demands to maintain energy requirements through an insect based diet, and switch to a diet of earthworms (Beintema *et al.*, 1991).

Furthermore, Beintema *et al.* (1991) argue that small chicks are unable to exploit earthworms as their bills are not long enough to catch them. Our data suggests that small chicks are able to exploit earthworms from a very young age, but may well be dependent on them being 'available' near or on the soil surface. Further direct observations of foraging behaviour are required to ascertain the interaction between young chicks and earthworms.

Evidence for the need of a greater calorific intake is further provided by the decline in particular of Coleoptera with chick age, and whilst there is a change in dietary composition with chick age, this is a gradual process rather than a dietary switch as proposed in other studies. Beintema *et al.* (1991) showed that there was no noticeable change in arthropods in the diet, but there was a gradual increase in abundance of earthworm with age.

A pertinent question is whether Lapwings optimise the chance of chick survival by synchronising the peak hatching period to coincide with peak food availability. Whilst data on the underlying invertebrate availability is lacking due to fieldwork constraints in 2001, the evidence collected on earthworms may offer some insights to this fundamental question. Lapwing chicks hatched later in the breeding season have been shown to have reduced survival probabilities (Galbraith 1988a; Linsley 1999; This study, Chapter 5). Two possible explanations for this are the availability of food and the effect of weather. Evidence from this study would suggest that the commencement of the chick foraging period (late April) coincides with a time of peak earthworm abundance. However, there was no decline in earthworm chaetae in faecal samples with date, which suggests that even later hatched were able to utilise earthworms sufficiently. Alternatively, later hatched chicks may be having to spend more time foraging to maintain earthworm intake, leading to an increased susceptibility to predation or disease (although there is no published material to support this hypothesis). A time-budget analysis of chicks is required as is an assessment of prey intake to test this hypothesis. Time spent feeding is important for chicks, and adverse weather conditions can have serious consequences for chicks unable to regulate there own body temperature. Time-budget constraints for small chicks caused by wet and/or cold weather, are more likely for early hatched chicks (although low SMD may lead to highly profitable earthworms being more readily available). Whilst later hatched chicks may be negatively affected by dry periods (Beintema *et al.*,

1991; Beintema & Visser, 1989b) as a result of high SMD. Even short periods of dry conditions have been shown to have a negative impact on farmland arthropod communities, with a corresponding positive effect of irrigation (Frampton *et al.*, 2000).

It seems likely that a trade-off exists between early nesting and synchronising the peak hatching period with optimal chick foraging conditions. Some plasticity in the timing of the breeding cycle is evident for Lapwings breeding in Dutch grasslands, where a shift in egg laying has been witnessed as a response to earlier agricultural operations (Beintema *et al.*, 1985).

The key findings from this chapter are

i) Earthworm biomass density differed between crop categories and tended to decline as the Lapwing breeding season progressed. Furthermore, earthworm biomass density declined following cultivation.

ii) Lapwing chick diet was varied, although there was a predominance of certain taxonomic groups, namely earthworms, Coleoptera and Aranae.

iii) There was a positive relationship between chick condition and the number of earthworm chaetae present in the diet. Furthermore, the number of earthworm chaetae in the diet increased with chick age. The frequency of Coleoptera and Aranae in the diet declined with chick age.

iv) The number of earthworm chaetae in the diet had a positive effect on chick growth rate.

CHAPTER 7

GENERAL DISCUSSION AND CONSERVATION IMPLICATIONS

This concluding chapter aims to

i) review the main findings of this thesis on a chapter by chapter basis and put them into a conservation context.

ii) make recommendations to improve the Arable Stewardship 'Lapwing' prescription.

iii) identify gaps in current knowledge and recommend future research priorities.

7.1 REVIEW OF FINDINGS

The quantitative assessment of aspects of Lapwing breeding ecology in this study identifies a number of key areas which are likely to add to our knowledge of understanding the demography underpinning the species' decline. Furthermore, interpreting the results of this research in the context of existing knowledge, identifies consistent patterns that assist in understanding the reasons behind the decline in Lapwing populations.

7.1.1 Chapter 2: Clutch initiation dates, clutch characteristics and hatching rates

The key result from this chapter concerns the period of peak nest initiation. This is particularly important in the context of Lapwing populations associated with agricultural habitats as the species is highly susceptible to nest loss from agricultural operations. The peak nesting period in this study was between 21st March and 19th April, and is comparable to nest initiation dates from other studies (Galbraith, 1988a; Hegyi, 1996; Shrubb, 1990). This suggests that agricultural operations should be encouraged, where appropriate, to be completed by the 20th March (approximately). The Option 1B prescription stipulates that the cultivation of the false seed-bed should be undertaken between 1st and 20th March, which should avoid all but the earliest of nests. The earliest nest was initiated on the 16th March, and only 6 nests in total were initiated prior to the 21st March. Alternatively, where late agricultural operations can't be avoided due to unfavourable weather conditions, or for late sown crops such as maize, keeping the 'cultivation window' as short as possible should prevent the destruction of both initial nests and subsequent replacement clutches.

For example, in 2000 a maize stubble field was ploughed in mid April, leading to a loss of four first nests. The field was left for two weeks and the seedbed was prepared leading to the loss of three replacement clutches. Subsequently, after a further two weeks the maize crop was drilled leading to the loss of a further replacement clutch. Lapwings have been shown to lay replacement clutches within ten days, and hence it is recommended to try to complete all operations from stubble ploughing to drilling within this ten day cultivation window. Furthermore operations such as rolling should be avoided for up to six weeks to enable egg laying, incubation, and the early stages of chick growth to be completed.

Although there has been a significant increase in clutch size for Lapwings as determined from nest record cards (Chamberlain & Crick, *in prep*), it is highly unlikely that this has had any substantial effect on overall breeding productivity. Indeed, this phenomenon of increased clutch size has been noted in other declining farmland birds and may be a density dependent response or because the remaining individuals or habitats are of high quality.

There is no long term data on clutch volume or hatching rates with which compare the results of this study, but it does seem unlikely that the large population declines witnessed in recent years are being driven by changes in clutch characteristics.

7.1.2 Chapter 3: Factors affecting nest-site placement at different spatial scales.

Successes in bird conservation through the use of agri-environment schemes have to date been limited to species which are rare with a limited range, eg Cirl Bunting *Emberiza cirlus* (Evans 1997), Corncrake (Aebischer *et al.*, 2000), and Stone Curlew (Aebischer *et al.*, 2000). The big challenge is to replicate these successes to birds that have more wide-ranging national distributions. This study suggests that prescriptions for the provision of Lapwing nesting habitat should aim to provide a short, patchy sward structure. Within arable landscapes this could involve the provision of fallow fields where fields are taken out of production, replicating the traditional low input farming practices typical of early twentieth century agriculture. Within such fields, rapid regeneration of weed species and volunteer crops may result in the land becoming unsuitable. Management to prevent this could involve a second cultivation, but this may well lead to losses of

existing nests (or chicks). The use of herbicides may reduce weed growth but this may be at odds with wider conservation goals. In the pilot Arable Stewardship Scheme, the Option 1B prescription stipulated that the fallow be preceded by a cereal or linseed stubble. The use of set-aside land following sugar beet was an important Lapwing habitat in this study, probably due to the use of broad-spectrum, pre-emergence herbicides that led to reduced weed growth the following season. This resulted in a patchy and short vegetation mosaic. Use of pre-harvest herbicides in linseed also led to a reduction in weed growth in the following year, and breeding Lapwings occurred on three out of three fields where Option 1B followed a linseed stubble in 1999 (changes in E.U. price support mechanisms resulted in very little linseed being grown in 2000 resulting in all Option 1B following cereal in 2001). The retention of over-wintered stubbles will encourage spring cropping, providing nesting habitat for Lapwings, as well as far reaching conservation benefits for a variety of seed-eating passerines. The targeting of management prescriptions should be encouraged to take in to account field boundary composition and distance to suitable chick foraging areas. For example, the siting of Lapwing nests is known to be strongly influenced by the proximity of grassland habitats (Galbraith 1988, Wilson *et al.* 2001), although this was less apparent in this study. Furthermore, chick survival is also negatively associated with distance to foraging areas (Galbraith, 1988) and although the provision of nesting habitat through agri-environment schemes is desirable, without consideration being given to the availability of chick foraging habitat, any benefits to Lapwing breeding productivity and hence populations are likely to be limited. The incorporation of Option 1B into the Countryside Stewardship Scheme, alongside the existing grassland prescriptions offers the potential for the provision of nesting and chick rearing habitat on the same landholding.

Furthermore, the 1999 payment rate for Option 1B provided to farmers through the Arable Stewardship Scheme was £540 per hectare (MAFF 1998). Hence, the financial cost of delivering Option 1B nation-wide is likely to limit the amount of land that can be given over to providing specific Lapwing breeding habitat. The general provision of over-wintered stubbles (the Arable Stewardship Scheme payment in 1999 was £55 per hectare) may have far reaching conservation benefits for a wide variety of farmland species, and would encourage spring cropping which is

suitable as Lapwing breeding habitat. The provision and targeting of the more expensive Option 1B habitat in areas with good Lapwing populations and the provision of over-wintered stubbles on a national scale should provide a balanced and cost effective approach to assisting in reversing the Lapwing population decline witnessed in the last two decades.

7.1.3 Chapter 4: Nest survival

The two prime causes of nest loss in this study were predation and agricultural operations, and consequently any conservation measures should aim to address these issues. The Lapwing's preference for spring tillage has been shown in a number of studies, which seems at odds with the poor breeding success associated with these fields in this study. Nest survival was particularly low on spring cereals and stubbles, although spring crops such as sugar beet had high survival estimates. Losses of nests on spring tillage were primarily associated with agricultural operations, which generally coincide with the peak nesting period of Lapwings (Chapter 2, Figure 2.1). With the Option 1B prescription a limit on the timing of agricultural operations (cultivations must be completed prior to 21st March) appears to have positive benefits, as no losses of nests on 1B fields were attributable to farming operations.

The large difference in nest survival between those nests <50m away from field boundaries and those >50m suggests that conservation measures should aim to provide habitat that is sufficiently distant from field boundaries to have a positive effect on nest survival rates. However, the effectiveness of such a measure in reducing predation pressure is likely to depend on the type of predator, but for reduction of corvid predation increasing the distance of nests from potential perches should be beneficial.

Although Lapwings are able to lay several replacement clutches, which may compensate nest loss, in areas where crop growth may be rapid, suitable nesting habitat becomes increasingly scarce as the breeding season progresses. It is important to note, however, that the overall survival rate in this study is better than that for many previously published estimates for the species.

7.1.4 Chapter 5: Chick growth, condition, survival and foraging habitat associations

As with many other recent studies of Lapwing breeding ecology, chick survival in this study was low. A relatively stable clutch size and high nest survival rates, would suggest that poor chick survival is the main factor leading to low breeding productivity. Although a degree of caution is required when interpreting the productivity estimates due to the lack of knowledge on re-nesting behaviour following clutch failure. The underlying reason behind poor chick survival remains unclear, although predation appears to be significant. However, there is some evidence to suggest that poor chick condition increases the susceptibility to predation. The positive relationship between the number of earthworms in chick diet and condition would suggest that improving the quality of foraging habitat could increase survival, although this requires further detailed investigation. Chicks that hatched on Option 1B were likely to remain in natal fields until they reached fledging age, which suggests that Option 1B could be suitable as both nesting and chick rearing habitat. However, to maximise benefits to breeding Lapwing Option 1B should where possible be placed adjacent to grazed pasture to provide optimal breeding habitat conditions. Outside of agri-environment measures, two other widely used habitat types for chick rearing were sugar beet and rotational set-aside, and similarly locating these to pasture should maximise benefits.

7.1.5 Chapter 6: Lapwing chick diet and earthworms

This study highlights the importance of earthworms not just as a component of chick diet, but also through their effect on chick condition and growth rates. Two practical solutions that should increase earthworm biomass are minimal tillage practices and inputs of farmyard manure. Minimal tillage cultivation techniques are known to have a positive effect on earthworm biomass, but are likely to be increasingly utilised in the future as a method of reducing inputs and on-farm costs. Current research is underway to assess the effect of minimal tillage on food resources for birds (Cunningham *et al.*, 2002). Switching from inorganic fertilisers to FYM should be encouraged where practical, which would have the dual benefit of improving soil structure, and would increase organic matter content within soils, thus stimulating sub surface activity of earthworms and

increasing their availability to Lapwing chicks and adults. Furthermore, agri-environment prescriptions aimed at raising water levels in grassland habitats may have potential benefits in terms of maintaining a low SMD and thus increasing availability of earthworms near the soil surface.

Other agricultural practices such as reduced pesticide inputs, and the promotion of a diverse sward structure both in grassland and arable crops are likely to lead to an increase in invertebrate biomass (Morris, 2000), but may be at odds with good agronomic practice leading to an economic loss to landowners.

7.2 RECOMMENDATIONS FOR OPTION 1B IN FUTURE AGRI-ENVIRONMENT SCHEMES

1) The cultivation date stipulated by the current Option 1B prescription avoids the peak nesting period for Lapwings. However, there may be a requirement for some flexibility when applying this prescription on a national basis. Climatic differences further north may make cultivation difficult during early March, and cultivation may need to be delayed until the end of March or early April depending on soil conditions. If nesting Lapwings coincide with cultivation, two options should be considered. Firstly, cultivation could be delayed until all nests have reached the hatching stage. Providing there is no danger to chicks (or other species such as skylark), a cultivation in May could extend available nesting habitat to other failed breeders. Alternatively, nests should be located, marked (using canes/sticks) and, either moved, or avoided, during the cultivation operations.
2) During the course of this study it was noted that a number of Option 1B fields had a rapid re-generation of vegetation and quickly became unsuitable as breeding habitat for Lapwings. In these instances farmers should be allowed to undertake an extra cultivation, providing this wouldn't be detrimental to other ground nesting birds.
3) The choice of crop that Option 1B can follow was limited to cereal and linseed.[1] It was noted in this study that sugar beet stubbles left as set-aside, particularly in the Cambridge area, were utilised by breeding Lapwing. The use of pre-emergence herbicides on sugar beet leads to reduced weed growth in the following season, resulting in a favourable sward for Lapwings. Option 1B should be allowed to follow sugar beet, and other crops such as potatoes, where Lapwings are identified as a priority species.
4) The Option 1B prescription does not allow the spreading of fertiliser, manure, lime or agrochemicals. A light application of FYM in the spring prior to the cultivation operation, may help stimulate earthworm activity near the soil surface. This could have benefits for both pre-laying females and chicks.

5) The average field size for Option 1B fields that had breeding Lapwings was just less than 4ha (Table 3.9). This is recommended as the minimum field size for Option 1B. However, smaller patches within the centre of fields would be beneficial.[2] To enhance nest survival, the Option 1B prescription should only apply to fields with low boundaries, or those that do not border woodland, or contain predator perches such as in field trees and telegraph poles.

6) Option 1B is aimed at providing nesting habitat for Lapwings, but to maximise benefits fields should be adjacent to suitable chick rearing habitat, such as cattle grazed pasture. Although in some areas where pasture may be scarce, Option 1B may be able to provide both nesting and chick rearing habitat, but this requires further research.

[1] Since Option 1B has been incorporated into the Countryside Stewardship Scheme as Option OS3, only a cereal crop can precede the spring/summer fallow period

[2] 2ha blocks of cultivated set-aside within fields have been used as a conservation measure for stone curlew. These blocks of set-aside can attract high densities of breeding Lapwing (R Winspear, *pers. comm.*)

7.3 AREAS OF PRIORITY RESEARCH

1) A greater understanding of re-nesting behaviour, and how habitat availability influences the ability to lay replacement clutches, is required to determine more accurate breeding productivity estimates.

2) A better knowledge of how chick foraging efficiency and prey availability are influenced in agricultural landscapes is required. An assessment of how crop growth, sward density and structure influences, not only prey availability, but also accessibility, and ultimately chick survival.[3] The development of a methodology to supplementary feed Lapwing chicks in the wild would enable us to test the importance of food availability on chick growth and survival.

3) A simple experiment is required investigating the effects of nest moving and nest avoidance during agricultural operations. This should be undertaken to determine methods of best practice.

4) Applications of FYM could have positive effects on earthworm abundance and thus may be a practical way of influencing food availability for chicks. An assessment of the effects of FYM on chick food availability, chick condition and survival is required.

5) Although there is no published evidence to suggest that either radio-tagging or colour ringing of chicks has an impact on survival, growth or behaviour, an analysis of existing datasets should be undertaken to determine that neither method is having a detrimental effect.

[3] As part of this thesis, this work was planned for 2001 but was cancelled due to the Foot and Mouth outbreak

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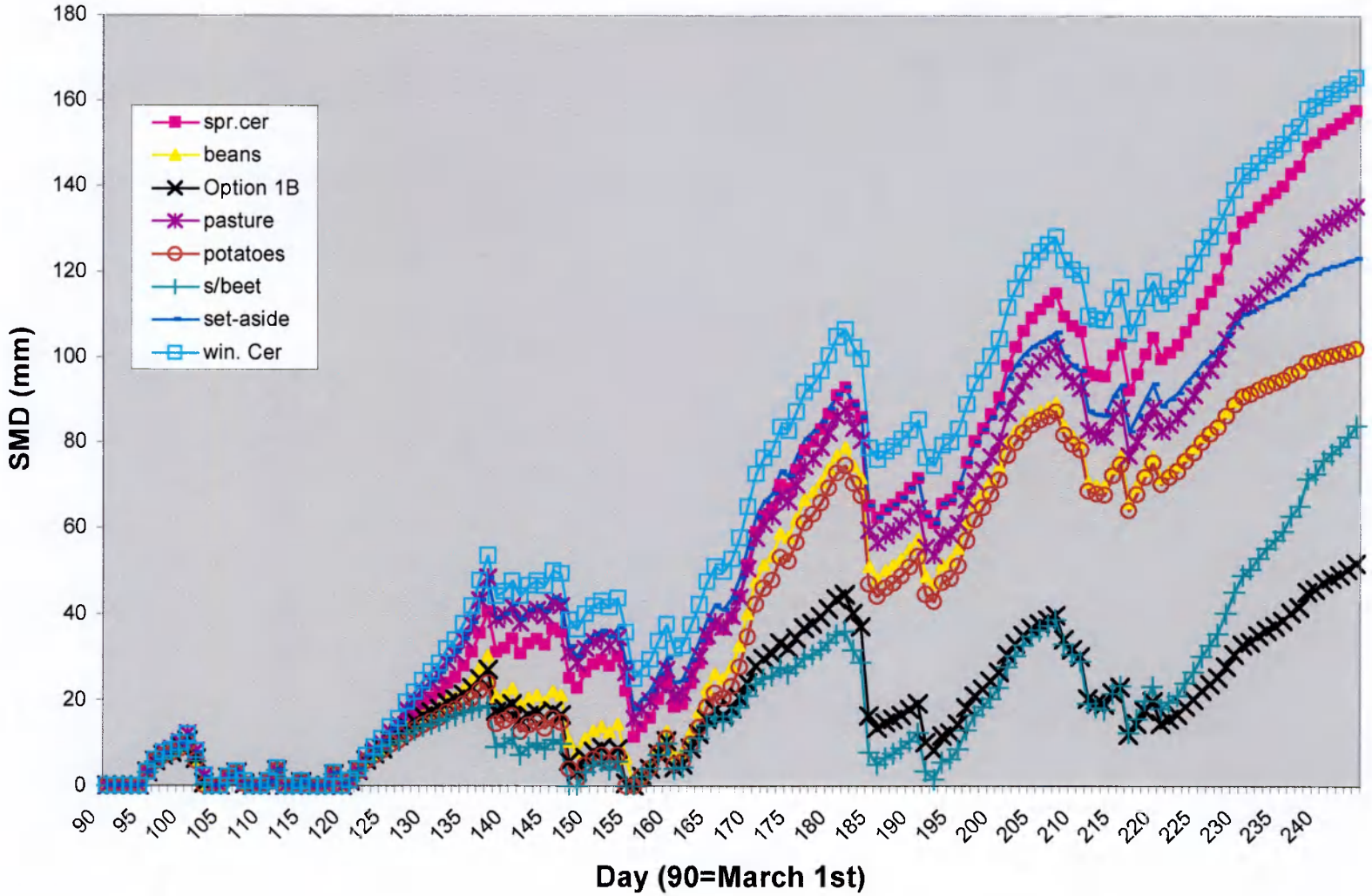
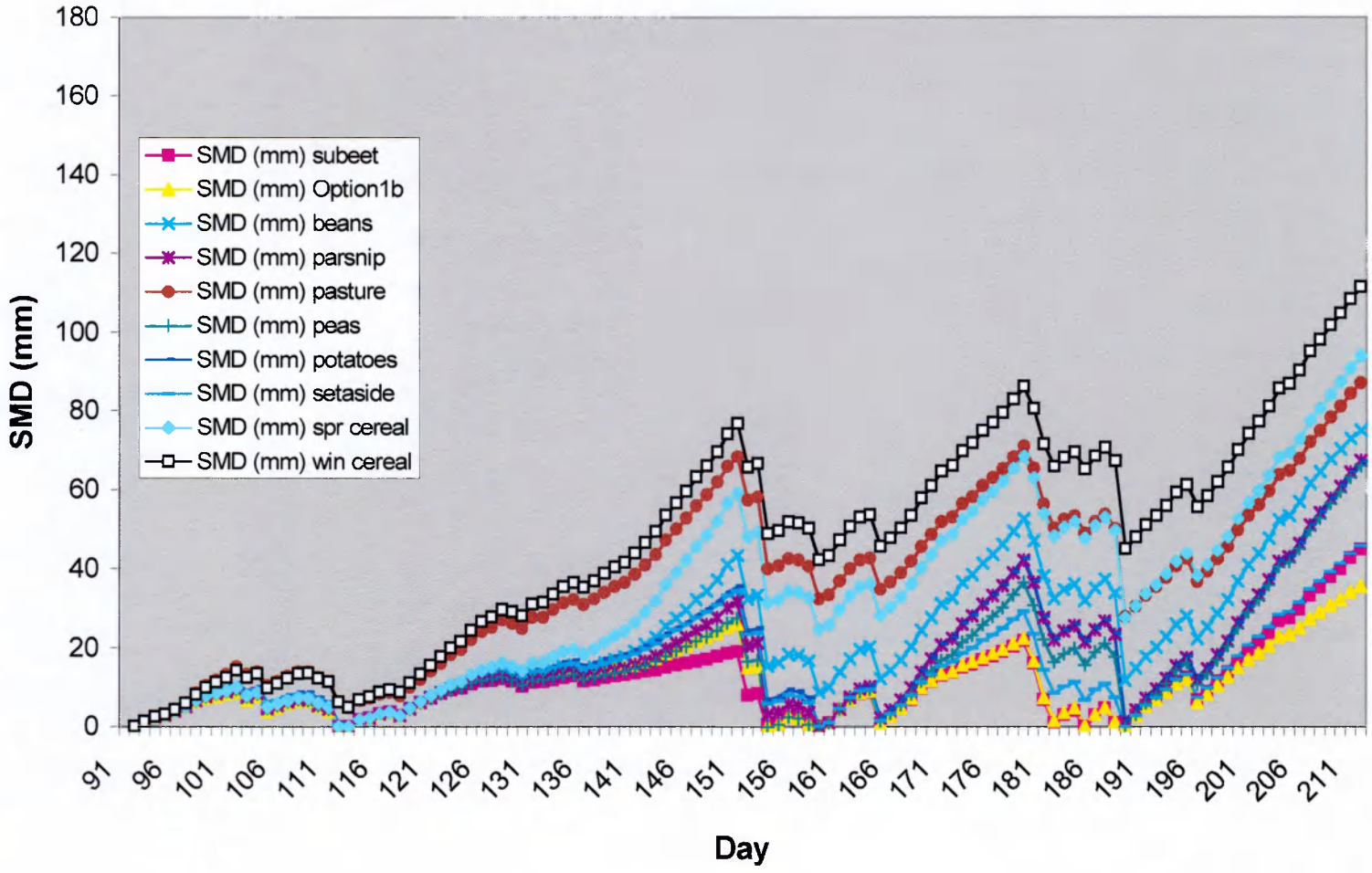
Appendix 1. Summary of Arable Stewardship options that have been incorporated into the main Countryside Stewardship Scheme.

Option	Description	Previous Arable Stewardship reference
Over-wintered stubbles		
OS1	Over-wintered stubble followed by a spring crop	1C
OS2	Over-wintered stubble followed by a low input spring cereal	
OS3	Over-wintered stubble followed by a spring/summer fallow	1B
Conservation headlands		
CH1	Conservation headlands with restricted use of insecticides and herbicides	3A
CH2	Conservation headlands with no fertiliser and restricted use of insecticides and herbicides	3B
Wildlife mixtures		
WM1	Wild bird seed mixture	5
WM2	Pollen and nectar mixture	5

Appendix 2. Soil Moisture Deficit (mm) by crop type in the Shropshire study area 2000.



Appendix 2 (cont'd). Soil Moisture Deficit (mm) for Cambridge 1999



Appendix 3. Farm characteristics and crop composition of farms used in the Shropshire study area.

Analytical group	Farm	Hectares surveyed	Average field size (n=fields)	Winter crops (ha)	Spring crops (ha)	Grass (ha)	Stewardship farm	Option 1B (ha)
1	LDRAY	111.9	7.5 (15)	52.7 (47%)	27.1 (24%)	14.0 (13%)	✓	4.0
	BICK	262.2	8.5 (31)	124.7 (48%)	74.0 (28%)	30.2 (12%)	✓	6.4
	total	374.1	8.1 (46)	177.4 (47)	101.1 (27%)	44.2 (12%)		
2	CHILL/RENS	371.0	7.7 (48)	241.3 (65%)	54.5 (15%)	55.7 (15%)	✓	6.6
3	HEXT	29.1	5.8 (5)	10.8 (37%)	-	13.8 (47%)	✓	6.0
4	NEWG	37.8	6.3 (6)	10.8 (28%)	6.8 (18%)	20.3 (54%)		
	GUILD+TOMK	90.3	5.0 (18)	9.1 (10%)	65.0 (72%)	4.5 (5%)	✓	4.0
	total	128.1	5.3 (24)	19.9 (22%)	71.8 (56%)	24.8 (19%)		
5	TRAC	7.5	3.8 (2)	4.0 (53%)	-	3.5 (47%)		
	KNIG	112.8	8.7 (13)	52.9 (47%)	28.3 (25%)	12.8 (11%)		
	FLAS	49.4	9.9 (5)	8.9 (18%)	36.5 (74%)	-		
	WJON	19.4	9.7 (2)	10.1 (52%)	-	-		
	BUTT	168.7	6.8 (25)	52.0 (31%)	16.0 (9%)	-	✓	
	total	357.8	7.6 (47)	127.9 (35.8%)	80.8 (23%)	16.3 (5%)		
6	WICK	107.4	6.0 (18)	7.9 (7%)	50.6 (47%)	20 (19%)	✓	11.2
	BUILD	16.8	5.6 (3)	4.8 (28%)	-	4.8 (28%)	✓	
	total	124.2	5.9 (21)	12.7 (10%)	50.6 (41%)	24.8 (20%)		
7	MANOR	26.1	4.4 (6)	10.3 (39%)	9.5 (36%)	2.0 (8%)	✓	4.3
	DAIRY	12.5	6.3 (2)	4.8 (38%)	-	-		
	total	38.6	4.9 (8)	15.1 (39%)	9.5 (25%)	2.0 (5%)		

Cont'd

8	NEWT	71.3	7.1 (10)	9.3 (13%)	60.0 (84%)	2 (3%)		
	OLDI	118.6	7.4 (16)	82.2 (69%)	36.5 (31%)	-		
	CATS	79.4	8.8 (9)	3.9 (5%)	75.5 (95%)	-		
	total	269.3	7.7 (35)	95.4 (35%)	172 (64%)	2 (1%)		
9	BEOB	218.8	7.8 (28)	47.5 (22%)	133.8 (61%)	14.8 (7%)		
	SPICE/OVEN	50.8	6.3 (8)	-	40.5 (80%)	5.5 (11%)		
	total	269.6	7.5 (36)	47.5 (18%)	174.3 (65%)	20.3 (8%)		
10	UDAN	47.5	7.9 (6)	-	47.5 (100%)	-		
	SNELS	27.5	6.9 (4)	14.0 (51%)	13.5 (49%)	-		
	total	75.0	7.5 (10)	14.0 (19%)	61.0 (81%)	-		
11	LUTL/HAY	73.5	4.6 (16)	29.5 (40%)	4.5 (6%)	21.0 (29%)	✓	4.0
	STAN	63.4	5.3 (12)	4.3 (7%)	50.8 (80%)	-		
	total	136.9	4.9 (28)	33.8 (25%)	55.3 (40%)	21.0 (15%)		